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CONTINUING THE PLANT WORLD

OFFICIAL PUBLICATION OF THE
ECOLOGICAL SOCIETY OF AMERICA

Volume I—1920

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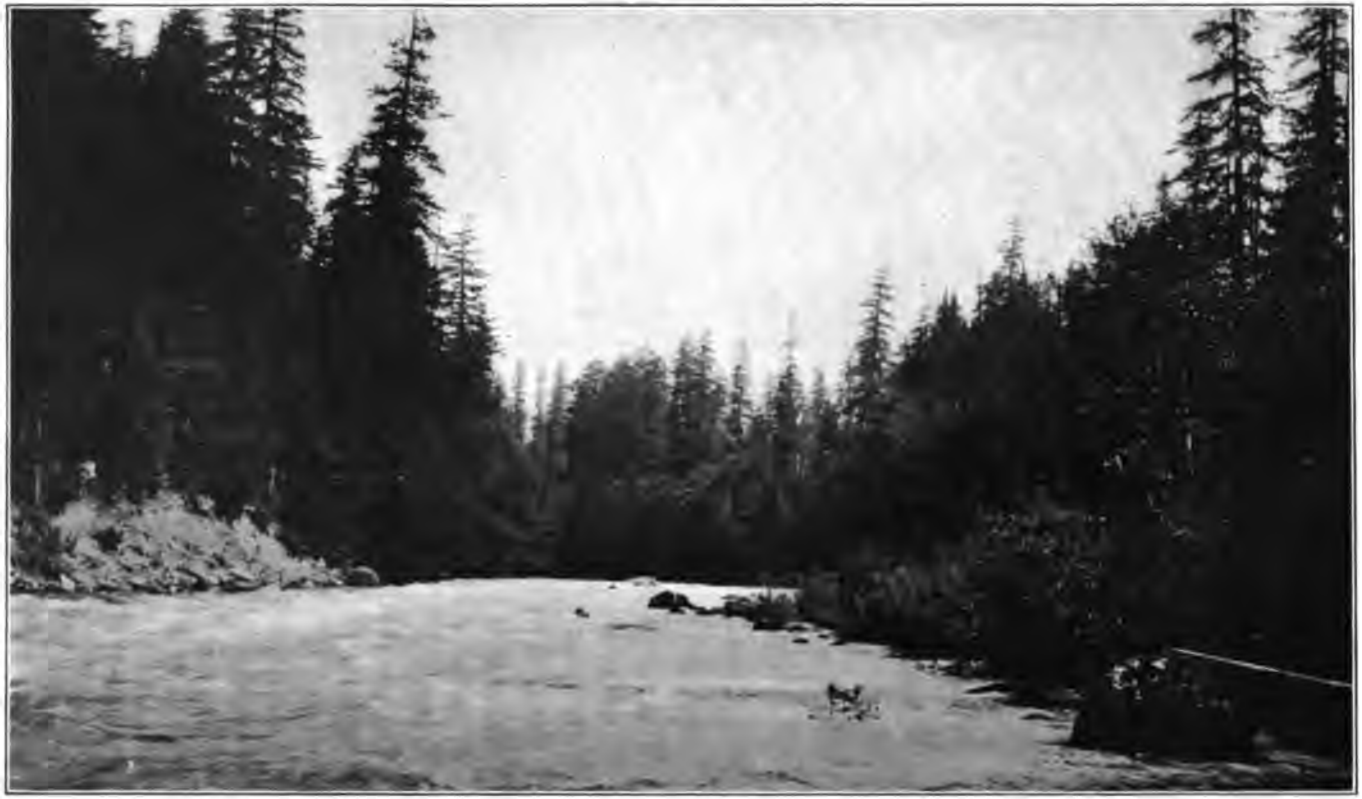
P. 169. Second paragraph, third line should read "concerned, the contents of the first pocket is alone of significance. Even"
P. 188. Plate VI should be Plate V, and Plate VII should be Plate VI.
P. 189. Plate VIII should be Plate VII.



Sauk River flowing through a mature forest of Douglas fir (*Pseudotsuga taxifolia*). Snoqualmie National Forest, Washington.
(See " The Establishment of a Douglas Fir Forest.")

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ECOLOGY

Vol. I JANUARY, 1920 No. 1

FOREWORD

THIS journal is issued to meet the demand for the collective publication of articles on ecology. Its pages are open to all who have material of ecological interest from whatever field of biology. While the variety of fields may cause diversity of treatment, yet the ecological significance of the papers will make them of general interest. Specialization is inevitable, but makes more urgent the need for cooperation. To approach different subjects from similar points of view is to lay the foundations of cooperation.

THE SCOPE OF ECOLOGY[1]

BARRINGTON MOORE

My purpose today is to draw your attention briefly to certain facts and tendencies in the field of ecology.

All life is controlled by two great forces, heredity and environment, and ecology is the science dealing with the environment. It therefore covers practically the whole field of biology, and is related in one way or another to every science which touches life.

There have been three stages in the development of the biological sciences: first, a period of general work, when Darwin, Agassiz and others amassed and gave their knowledge of such natural phenomena as could be studied with the limited methods at hand; next, men specialized in different branches, and gradually built up the biological sciences which we know today; and now has begun the third or synthetic stage. Since the biological field has been reconnoitered and divided into its logical parts, it becomes possible to see the interrelations and to bring these related parts more closely together. Many sciences have been developed to the point where, although the field has not yet been fully covered, contact and cooperation with related sciences are essential to full development.

Ecology represents the third phase. You have but to glance at the list of ecological problems drawn up by the Committee on Cooperation of the Ecological Society and appearing in Science for January 16, 1920. And this list is far from complete. You will see problems requiring work by zoologists, botanists, foresters, geographers, meteorologists, soil chemists, soil physicists, bacteriologists, and geologists, to mention only some of the leading lines.

What, precisely, is the significance of this synthesis? No man can be a highly trained zoologist, botanist, forester, and meteorologist all in one. It means that the ecologist, though he specializes on animal ecology or plant ecology, must take the broad ecological point of view of his problem. He must be able to see all its aspects and how it is related to each of the sciences which can aid in its solution. In this way he will be enabled to carry the problem himself as far as his own field and training permit, and secure the cooperation of workers in related fields for those parts which he is unable alone to cover. For example, a forester is confronted with the reforesting of ten thousand acres of burned-over mountains. He begins by using data already accumulated bearing on his problem, but this is not enough. He secures the cooperation of a meteorologist in order to get accurate data on climate; he calls in a soil specialist to determine the suitability of the different soils for the different tree species; he asks the assistance of a zoologist in protecting his sowings from damage by rodents; he cooperates with the phytopathologist in overcoming fungous attacks, and so on.

---

[1] Presidential address delivered before the St. Louis meeting of the Ecological Society of America, December 31, 1919.

There is hardly a science which has not been influenced by the ecological point of view, for ecology is new in name but not in fact; it is superposed on the other sciences, not an offshoot as phytopathology grew out of botany.

Our point of view toward ecology should be determined by consideration of what it is doing in all the fields of biology, whether in its own or under some other name. All agricultural research, except breeding, is ecology. To garner successful harvests it is necessary to know the relation of the cultivated plant to its environment. Investigations in alkali and drought resistant crops have added thousands of acres to the farms and homes of the country. The workers in this field are gradually recognizing their connection with ecology. Should we not endeavor to hasten this recognition?

In animal industry ecology rendered marked service in its own name when an ecologist in the Forest Service, after several years of painstaking investigation, devised a method of restoring depleted grazing lands without the expense of artificial reseeding or the hardship of closing the range against grazing. Many thousands of sheep and cattle were permanently added to our supply through the work of this ecologist.

Foresters have long recognized that information on the relation of the forest to its environment lies at the basis of their practice; they have sought this information under the name of silvics; now such work is beginning to be known as forest ecology.

Geography, in so far as it is the study of man in relation to his environment, is human ecology. In the field of sanitation men are endeavoring to change a dirty environment into a clean and therefore healthy one. What is this but ecology? During the war one of the army camps was infested with mosquitoes. An ecologist was summoned. He experimented, and found a certain kind of fish, which when introduced into the neighboring ponds destroyed the mosquitoes.[2]

In the field of history, since the time of the great French historian Taine, there has been a growing tendency to correlate events with the influence upon man of his environment.

The foregoing instances will call to your minds many others showing the scope of ecology and its relation to the present trend of science. All the biological sciences demand research which is fundamentally ecological in character. Nobody can doubt that this demand will be even greater in the future.

---

[2] Hildebrand, S. F., "Fishes in relation to mosquito control in ponds," U. S. Dept. of Commerce, Bureau of Fisheries, Document 874, 1919.

How are we, as a Society, going to respond to this demand? Will we be content to remain zoolgists, botanists, and foresters, with little understanding of one another's problems, or will we endeavor to become ecologists in the broad sense of the term? The part we will play in science depends upon our reply. Gentlemen, the future is in our own hands.

THE CONTROL OF PNEUMONIA AND INFLUENZA BY THE WEATHER

ELLSWORTH HUNTINGTON

Research Associate in Geography in Yale University

1. THE NEW TREATMENT OF RESPIRATORY DISEASES

The revolutionary changes of the last few decades in the treatment of tuberculosis may be the precursors of an even more drastic revolution in the treatment not only of tuberculosis, but of pneumonia, influenza, and other respiratory diseases. The principle of the new tuberculosis treatment is the purely ecological idea that the respiratory system requires outdoor air. The logical expansion of this principle is that the best treatment for all kinds of respiratory diseases is air that is ideal in all respects. Aside from light and purity, the three most important atmospheric conditions are (1) temperature, (2) relative humidity, and (3) variability and movement. The old indoor treatment of tuberculosis was a failure largely because it centered entirely around temperature. The new outdoor treatment—although most people do not recognize this—centers around variability and movement with only incidental attention to temperature and humidity. The treatment of the future will presumably pay equal attention to all three factors.

The first step toward this new treatment is a statistical analysis of the relation of ordinary air to health. Hence the present paper is an attempt to find out what are the ideal atmospheric conditions for patients suffering from pneumonia and influenza.

2. RELATION OF TEMPERATURE TO PNEUMONIA AND INFLUENZA

To begin with temperature, Greenburg[1] has taken the monthly figures for deaths from lobar pneumonia in New York, Boston, Newark, and Providence for a series of years, and has compared them with the mean temperature of the corresponding months by means of "climographs." He finds that deaths from pneumonia have a direct relation to the outside temperature, and decrease systematically as the temperature rises. Shaw[2] states that in England the same rule applies to influenza under ordinary circumstances.

---

[1] David Greenburg, "Relation of Meteorological Conditions to the Prevalence of Pneumonia," Journal of American Medical Association, 1919, p. 252.

[2] Napier Shaw, Quarterly Journal, Royal Met. Soc., Vol. XLV, July, 1919. (In discussion of article on Atmospheric Conditions which Affect Health, by Leonard Hill.)

In order to test the matter in another way, I have taken the day instead of the month as the unit, and have tabulated the deaths from lobar and broncho pneumonia according to temperature, as appears in Table 1.

TABLE 1. *Average daily deaths from pneumonia at various mean temperatures in New York City, from April, 1917, to March, 1918*

Mean Temp. Fahrenheit . .	20° or less	21°–32°	33°–45°	46°–55°	56°–65°	66°–70°	71°–75°	Over 75°
Lobar pneumonia . . .	26.5	26.4	27.8	20.6	17.4	9.4	6.3	6.7
Broncho pneumonia .	8.3	9.6	8.2	6.2	5.4	3.9	2.5	3.3
No. of days	(30)	(47)	(72)	(70)	(51)	(31)	(38)	(26)

The general decline in the deathrate with rising temperature is obvious. From 33° to 75° it is highly systematic. At the lowest temperatures there is a little irregularity, due to the fact that a mild epidemic doubled the deathrate for a couple of weeks at the end of March. In view of the lateness of the season at which this occurred, it is surprising that the deathrate at temperatures of 33–45° has not been raised much higher. In ordinary years the realtion between low temperature and the deathrate wolud be even stronger than appears in Table 1. At the right-hand end of the table, a slight increase in deaths is apparent at high temperatures above 75°. Judging by more abundant statistics for other diseases, this is a constant characteristic, and means that high temperatures as well as low are bad for pneumonia.

As a test of Shaw's conclusion that influenza as well as pneumonia varies inversely as the temperature, I have used the weekly figures for deaths from influenza in New York City during the thirty years from 1889 to 1918. These are summed up in Figure 1, where the solid line shows the average weekly deathrate from influenza omitting the great epidemics of 1891 and 1918, but including the minor epidemics. It is noticeable that deaths from influenza begin toward the end of September at about the time when the nights first become frosty. The deathrate suddenly increases about the middle of December at approximately the time when the mean temperature falls below freezing. It reaches a maximum a little after the middle of January, just at the time when the cold weather also reaches a maximum. Thereafter the disease declines, the decline being regular at first for a month, but then becoming irregular because of epidemics. If these epidemics were eliminated, it seems probable that the deathrate would follow the dash line in Figure 1, and be reduced to zero at about the time when the frosts come to an end. However this may be, it is quite clear that aside from the two great epidemics, influenza begins with the frost; becomes severe when the temperature averages below freezing; reaches a maximum when the weather is coldest; and then declines.

The dotted lines in Figure 1 show how the average weekly deathrate for

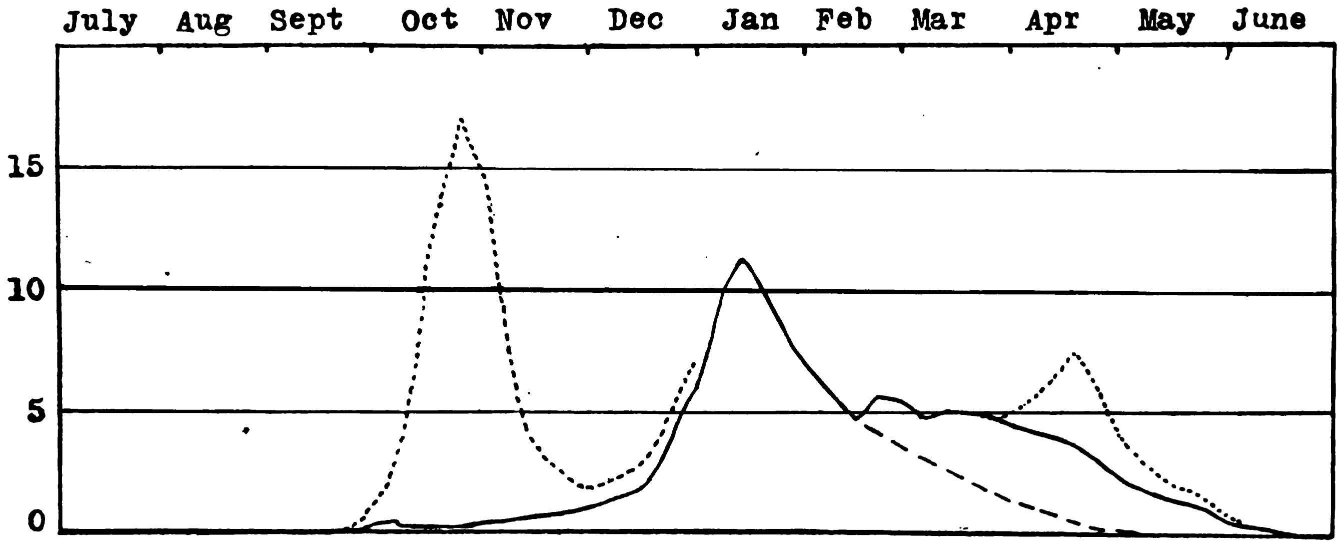

FIG. 1. Weekly deathrate per million from influenza in New York City from 1889 to 1918. Solid line indicates deathrate omitting the epidemics of 1891 and 1918. Dotted line indicates deathrate when these two epidemics are included. Dash line indicates probable deathrate if other epidemics were omitted.

the thirty years is modified if the two great epidemics are included. We shall return later to the contrast between the epidemic and endemic forms of influenza. For the present it is enough to see that the endemic form and even the milder epidemics in New York agree with Shaw's conclusion as to the marked effect of low temperature in increasing the severity of influenza.

3. Relation of Humidity to Pneumonia and Influenza

Let us now turn to humidity. In all the investigations of pneumonia except Greenburg's, relative humidity has been omitted or has played a minor rôle. Greenburg, however, find that the amount of moisture in the air is of the highest importance, for at all temperatures there are fewer deaths when the relative humidity is high than when it is low. The daily deaths in New York City from April, 1917, to March, 1918, lead to the same conclusion, but give an important emphasis to certain temperatures. This appears in Table 2.

The first section of the table, headed "Weather Conditions," shows that here, as in Table 1, the days of the year have been divided into eight groups according to temperature. Each group has again been divided into two divisions: (I) days with low relative humidity, and (II) days with high relative humidity. For temperatures below 65° the dividing line has been a humidity of 60 percent, while for higher temperatures, in order to make the number of days in the two sections more nearly equal, it has been 70 percent. Section 2 shows the number of deaths per day from lobar pneumonia on the day when the given weather conditions prevailed. In each of the eight temperature groups, the days with a high relative humidity have an advantage, as appears in the line labelled "Advantage of II over I." This ranges from 0.8 percent up to 26.8 percent. In Section 3 similar figures are given for the number of deaths on the day *after* the given weather conditions. Here, just as in Section 2, the days with high relative humidity have a decided advantage. In other words, no matter what the temperature, the deathrate from lobar pneumonia during the year in question was less when the humidity was high than when it was low.

The reader may ask whether the apparent effect of humidity may not be really due to temperature. This is answered in the next to the bottom line of Section 1, which shows that in six groups out of eight the difference between the temperature of the days with high and low humidity is only about one degree. The two exceptional groups are the coldest and the warmest. In the cold group the days with high humidity were 3.2° F. colder than those with low humidity, which would tend to make the deathrate of the more humid days higher than that of the others instead of about 7 percent lower, as is actually the case. Apparently a little extra moisture more than overcomes the bad effects of a few degrees of cold. Turning to the warmest group, we find a different state of affairs. Extremely high temperature, as

TABLE 2. *Daily deaths from pneumonia in relation to temperature and humidity, New York City, April, 1917, to March, 1918*

Section 1. Weather Conditions

Mean temperature	20° or less	21–32°	33–45°	46–55°	56–65°	66–70°	71–75°	76° or more
I. Days with Low Rel. Humidity:								
A. Av. Temp.	13.9°	27.1°	38.9°	49.8°	61.0°	68.1°	72.8°	79.4°
B. Av. Rel. Hum.	50.9 %	52.6 %	50.6 %	48.2 %	49.2 %	57.6 %	57.0 %	64.0 %
C. No. of Cases	16	31	38	38	21	16	21	15
II. Days with High Rel. Humidity:								
A. Av. Temp.	10.7°	27.8°	39.7°	49.6°	60.4°	66.8°	73.1°	77.1°
B. Av. Rel. Hum.	71.1 %	78.1 %	72.4 %	73.7 %	76.4 %	82.5 %	78.0 %	77.9 %
C. No. of Cases	14	17	34	33	30	15	17	11
Excess of II over I:								
A. Temp.	−3.2°	0.7°	0.8°	−0.2°	−0.6°	−1.3°	−0.3°	−2.3°
B. Rel. Hum.	20.2 %	25.5 %	21.8 %	25.5 %	27.2 %	24.9 %	21.0 %	13.9 %

Section 2. Deaths per Day from Lobar Pneumonia on *Same* Day as Given Weather Conditions

I. Low Relative Humidity	27.5	26.5	28.2	22.4	20.3	10.6	6.7	6.8
II. High Relative Humidity	25.4	26.3	27.3	18.4	15.9	8.1	5.9	6.5
Advantage of II over I	7.6 %	0.8 %	3.2 %	17.8 %	21.6 %	23.6 %	26.8 %	4.4 %

Section 3. Deaths per Day from Lobar Pneumonia on Day *After* Given Weather Conditions

I. Low Relative Humidity	29.3	26.8	29.2	20.6	19.3	10.4	6.2	6.7
II. High Relative Humidity	27.2	25.5	28.6	19.2	14.3	8.2	6.2	6.5
Advantage of II over I	7.2 %	4.9 %	2.1 %	6.8 %	25.9 %	21.2 %	0.0 %	3.0 %

Section. 4. Deaths per Day from Broncho Pneumonia on *Same* Day as Given Weather Conditions

I. Low Relative Humidity	9.4	9.2	7.7	6.4	5.9	3.6	2.6	3.7
II. High Relative Humidity	8.8	10.2	8.7	6.0	5.0	4.2	2.4	2.8
Advantage of II over I	6.4 %	−10.9 %	−13.0 %	6.2 %	15.3 %	−16.7 %	7.7 %	24.4

Section 5. Deaths per Day from Broncho Pneumonia on Day *After* Given Weather Conditions

I. Low Relative Humidity	10.0	9.8	7.3	6.3	5.9	4.0	2.8	3.3
II. High Relative Humidity	8.9	9.6	7.9	6.1	5.0	4.1	2.7	2.9
Advantage of II over I	11.0%	2.0%	−8.2 %	3.2 %	18.0 %	−2.5 %	3.6 %	12.1 %

we have already seen, is harmful. Thus the days with high humidity have an advantage of 2.3° in temperature when compared with the dry days. Nevertheless, their deathrate is less by only 4.4 percent in Section 2 and 3.0 percent in Section 3. This slight advantage is probably due entirely to the lower temperature of the moister days, and it is doubtful whether high humidity is any advantage in such warm weather. From other lines of evidence such as operations, we infer that high humidity and extremely low humidity are about equally harmful at high temperatures.[8] The best condition is intermediate.

4. Divergent Humidity Relations of Lobar and Broncho Pneumonia

Turning now to Sections 4 and 5 of Table 2 we find that humidity appears to be of much less importance in broncho pneumonia than in the lobar type. Not only is there a good deal of irregularity in the numbers showing the advantage of moist over dry days, but five out of sixteen of the numbers are negative. Doubtless much of this irregularity is because the deaths from broncho pneumonia numbered only 2,400 against 7,200 from lobar pneumonia. It seems likely, however, that there is a real difference between the two types of pneumonia, and that in the more severe and deep-seated form proper humidity is much more important than in the milder type. Nevertheless, the weighted average of all the groups of broncho pneumonia as given in Sections 4 and 5 shows that the days with higher humidity have an advantage of about 2 percent over the drier days.

5. Effect of Humidity at Indoor Temperatures

By far the most significant part of Table 2 is the two groups of days having temperatures of 56–65° and 66–70°. Such temperatures represent the conditions which prevail at all times within doors. Therefore, it seems justifiable to use them as a criterion of the actual effect of humidity upon patients. In lobar pneumonia the advantage of the days with high humidity at these temperature averages 23 percent, while even in broncho pneumonia the weighted average for sections 4 and 5 amounts to an advantage of about 7 percent for the days with the higher humidity. These figures go far toward indicating that a considerable part of the harm usually attributed to low temperature is really due to the low humidity which prevails within doors when the outside air is cold. When the outside air averages 55–70° and the relative humidity is above 70 percent. the deathrate from lobar pneumonia for the period under discussion remains fairly constant at about 11. At the same temperatures, if the humidity is between 40 and 50 percent, the daily deathrate rises to 17.8, or to about 14.5 if allowance is made for certain exceptionally warm days in early spring when the winter deathrate still prevailed. In other words, as long as the humidity remains above 70 percent or possibly 65 percent, the deathrate remains at a rather uniform and comparatively low level. A further drop of about 20 percent in humidity, however, causes an increase of at least a third in the deathrate.

---

[8] Huntington, Ellsworth, "Air Control and the Reduction of the Deathrate after Operations," Modern Medicine, Oct. and Nov., 1919, pp. 463–468, 555–558.

During the winter the air in the average house in New York has a relative humidity of only about 30 percent, while the deaths from lobar pneumonia number about 27 or 28 per day for the year under discussion. Suppose now that during the warm weather when the outside air averages 55–70°, the humidity were to be as low as in our winter houses. Apparently the pneumonia deathrate would increase by at least a third and perhaps one half over what it is in such weather when the humidity is 70 percent or more. Of course a far larger body of figures is needed before we can determine the exact effect of any given condition, but the principle seems clear. Apparently we are killing people by the thousand simply because we do not properly humidify the air in our hospitals.

It would be well if the method of Table 2 could be applied not only to pneumonia for many years, but also to influenza and many other diseases. On account of the lack of data for influenza except during the epidemic, however, this is at present impossible. Nevertheless, deaths from influenza and lobar pneumonia follow so closely the same course that it seems probable that conditions which are bad in one case are also bad in the other.

6. Relation of Variability in Temperature to Pneumonia

We come now to the relation between disease and the variability of the weather, a subject as to which there is almost no reliable information. Yet there appears to be a close relationship, as is indicated in Table 3. In this table the same data have been used as in Tables 1 and 2, namely, the daily deaths from lobar and broncho pneumonia for a year in New York City. Instead of employing the absolute number of deaths, however, the *change* from one day to the next has been taken, in order that the greater frequency of days with abrupt changes of temperature in winter than in summer may not confuse our results. Moreover, in any such investigation as this the most important thing is to discover what conditions cause a change one way or the other in the deathrate.

In Table 3 line *A* indicates that during the months from April to September there were fifteen days when the average temperature of the day was 6° or more in excess of the average for the preceding day. On these days there was an average decline of 1.60 in the number of deaths from lobar pneumonia and 1.00 from broncho pneumonia. In line *B* it appears that on the fifty-four days when the temperature rose 2° to 5°, deaths from lobar pneumonia increased 0.61, while those from the bronchial form decreased 0.21. In both cases the change in the deathrate was less than in *A*, and the conditions of health were not so good. With a change of temperature amounting to 1° or less, line *C,* and with a drop of only 2° to 5°, line *D,* we still find an increase in the deathrate. With a drop of 6° or more, however, line *E,* the lobar type of pneumonia shows a diminution of 1.55 in the deaths per day and the bronchial type of 1.30. Turning to the winter months from October to March, we find conditions like those for the six warmer months except that while a marked rise of temperature is better than little or no change, it is by no means so favorable as a drop. Table 3 is highly important because it departs so far from our ordinary assumptions. It seems to indicate that at all seasons a drop of temperature has a stimulating effect and thereby diminishes the deathrate. This drop must of course be distinguished from continuous cold weather which has been shown above to be unfavorable. A rise of temperature also has a stimulating effect, but not so marked or consistent as that of a drop, while days when there is little or no change in the weather are the most unfavorable.

TABLE 3. *Effect of variability of the weather upon deaths from lobar and broncho pneumonia in New York City, from April, 1917, to March, 1918*

Note.—The figures in the body of the table indicate the average amount by which the number of deaths increased or decreased on the days having the indicated changes of mean temperature. The change in mean temperature is the amount by which the average temperature for a given 24 hours is above or below that of the preceding 24 hours.

	April-September			October-March		
	No. of days	Change in deaths from pneumonia		No. of days	Change in deaths from pneumonia	
		Lobar	Broncho		Lobar	Broncho
A. Rise of 6° or more	15	−1.60	−1.00	43	−0.40	0.26
B. Rise of 2°–5°	54	0.61	−0.21	44	1.07	0.64
C. Change of 1° or less	50	0.04	0.34	25	1.32	0.80
D. Drop of 2°–5°	43	0.28	0.26	28	1.07	−0.89
E. Drop of 6° or more	20	−1.55	−1.30	42	−1.64	−1.21

7. CONFIRMATION OF PRESENT INVESTIGATION BY OTHER STUDIES

The results thus far given are interesting and suggestive, but not conclusive. They are confirmed, however, by other lines of evidence. For example, nine million deaths from all sorts of diseases in the United States, France, and Italy during a period of fifteen years show a relation of temperature and humidity closely similar to that of lobar pneumonia.[4] They indicate that the health of Americans and Europeans is best when the average temperature for night and day is 64° F. and when the average humidity is 80 percent. In the same way a study of the weather on the day of death for 400,000 cases in New York City during a period of eight years shows with surprising clearness that a drop in temperature, as distinguished from steady cold, is beneficial at all seasons. A rise of temperature is in general unfavorable, and in this respect the results from the 400,000 deaths in 8 years differ from those based on the 9,600 deaths from pneumonia in a single year. Nevertheless, both sets of data combine to indicate that weather with frequent changes of considerable magnitude in both directions is distinctly better than weather when there are only slight changes.[5]

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[4] Huntington, Ellsworth, "World Power and Evolution," Yale University Press, 1919.

8. Why Variability is Helpful

During variable weather, even when patients are in well-warmed houses, a drop in temperature stimulates by causing a decrease of the unfavorably high temperature which regularly prevails in our houses. It also causes much more movement of the air than at times when the weather stays stationary from day to day. The harm that comes from a rise in temperature at any season except summer is not easy to explain. Apparently it arises largely from the fact that when the outside air grows warm the inside is apt to run up to high levels, even 75° or more, a condition which is decidedly harmful. If this is the case, however, the benefit that apparently comes to pneumonia patients from a rise in temperature is puzzling. Possibly, during the year used in this article, the increased humidity which usually prevails when the temperature rises overcame the bad effects of increased warmth. Moreover, judging by Table 1, it may be that pneumonia patients are favored by a temperature somewhat higher than that which is best for most ailments.[6]

9. Summary of Most Favorable Conditions

Another confirmation of the general truth of the results here set forth is found in a study of surgical cases in Boston for five years at one hospital and ten at another.[7]

Operations stand much the best chance of success if performed under the following conditions: (1) an average temperature of about 65°; (2) air of high relative humidity, provided it is not too warm; (3) a drop of temperature; and (4) a general condition of frequent and pronounced changes from day to day.

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[5] See "World Power and Evolution" or a summary entitled "The Interpretation of the Deathrate by Climographs," Modern Medicine, Vol. 1, No. 1, May, 1919.

[6] The effects upon man in health as well as in sickness of a variable as compared with a uniform climate offer a fruitful field for research. A uniform climate such as that of Western Europe and the Pacific Coast of the United States has generally been considered just as healthy, if not as stimulating, as the variable climate of the North Atlantic seaboard of America. Is not the greater heat of American houses, in winter, as compared with European houses, an attempt to overcome sudden changes of temperature? Just what physiological effects does the variability produce, and what the uniformity? What part is played by the various factors, temperature, air pressure and atmospheric electricity?—Editor.

[7] Huntington, Ellsworth, "Air Control and the Deathrate After Operations," Modern Medicine, Vol. 1, 1919, Sept. and Nov.

The essence of the whole matter is that the human body seems to have a decided optimum of temperature, humidity, and variability, and to be highly sensitive to any departure from the optimum. Different diseases apparently shift the optimum a little in one direction or another; surgical cases may require great humidity at the time of the operation. and less later; lobar pneumonia may prefer a temperature a little higher than the optimum for persons in health; and other diseases may have their own peculiarities. Yet the general fact seems to be that in all diseases the departures of the air from the optimum are one of the greatest causes of death.

10. Data for Investigation of Epidemics of 1918

The next question which we shall consider is whether epidemic influenza and pneumonia show any climatic relationships at all similar to those of the endemic forms of the diseases. Nothing seems better established than that influenza epidemics may break out at any season, and that once started they run their course in spite of weather or climate. The only question is how far the conditions of the air may increase or diminish their severity. In the hope of getting some light on this problem, I have made use of the data stated in Table 4.

Table 4.[8] *Date Used in Investigation of Influenza Epidemic*

	Average Daily Change
1. *New York City.*	
A. Daily onset of cases of influenza, Sept. 18–Dec. 26, 1918	5.53
B.	
C. Daily deaths from influenza, Sept. 15–Nov. 25, 1918	15.20
D. Daily deaths from pneumonia, Sept. 14–Nov. 25, 1918	14.50
2. *Boston.*	
A. Cases of influenza reported daily, Oct. 4, 1918–Apr. 30, 1919	24.78
B. Cases of lobar pneumonia reported daily, Sept. 9, 1918–April 30, 1919	5.60
C. Daily deaths from influenza, Sept. 8, 1918–April 30, 1919	3.88
D. Daily deaths from pneumonia (all forms) Sept. 7, 1918–April 30, 1919	2.53

[8] The New York figures are more valuable than those of Boston for three reasons. (1) The number of cases is far larger than at Boston, although this is partly offset by the shorter period for which figures are available. (2) The relative humidity is the true mean of 24 hourly observations, and is not limited to a single observation morning or evening as at Boston. (3) Under heading *A* in the table the New York figures show the actual date when people began to feel seriously ill, whereas in Boston *A* and *B* represent merely the day when the physician was called, which of course introduces a certain error. Even in New York the records are far from ideal. As late as September, 1919, I could not procure a daily record except for the short period from September 14 to November 25, 1918. New York goes ahead of other cities, however, in preserving the report cards sent in by physicians, and in providing on them a space

In discussing the epidemic of 1918 I shall say nothing about mean temperature, for the period is too short to give any important results. On the basis of the evidence already cited, however, it seems safe to say that an epidemic in warm weather is much less severe than the same epidemic would be in cold weather.

In computing the effects of humidity and variability, I have reduced the exorbitant importance of the peak of the epidemic by using the *change* in the deathrate or case-rate from day to day, since that is what chiefly counts. Nevertheless the sudden onset of the epidemic is so obviously due to the virulence of the bacteria and not to the weather that it scarcely seems possible that any relationship should appear. Therefore, it is highly surprising to find that Tables 4 and 5 show strong signs of relationships like those found in the endemic forms of both influenza and pneumonia. In order to facilitate comparisons, the main figures in Tables 5 and 6 have been reduced to percentages of the average daily changes given in Table 4. Moreover, they are not the figures for a single day but the averages for the day on which a given weather condition occurred and for the succeeding day.

11. EFFECT OF VARIABLE WEATHER IN MITIGATING THE EPIDEMIC

TABLE 5. *Influenza and Pneumonia Compared with Changes in Temperature*
(Figures in parenthesis show number of days)

	Rise of 4° or more	Change of 3° or less	Drop of 4° or more
1. *New York.*			
A. Daily onset of influenza.......	21.2 (30)	10.3 (40)	−26.7 (23)*
B.	....	....	....
C. Daily deaths from influenza....	15.1 (21)	4.5 (31)	−28.2 (19)*
D. Daily deaths from pneumonia..	33.1 (21)	−1.4 (32)	−31.7 (19)*
2. *Boston.*			
A. Daily reports of influenza......	7.6 (58)	6.5 (75)	−19.2 (60)*
B. Daily reports of pneumonia....	11.3 (69)	−4.8 (83)	− 6.3 (64)*
C. Daily deaths from influenza....	−8.7 (74)	10.6 (91)	− 2.7 (69)
D. Daily deaths from pneumonia..	19.2 (77)	−1.7 (92)	−14.4 (66)*

We will take up variability before humidity, because it shows the more striking relationships. In Table 5 the first line means that in New York City during the period represented by *A* in Table 4 there were thirty days when the temperature averaged 4° or more above that of the preceding day. On those days and on the day immediately after there was an average daily increase of 21.1 percent in the number of new cases of influenza. In the next column it appears that on the 40 days with a change of 3° or less the deaths increased 10.3 percent, while the 23 days with a drop of 4° or more in temperature show an average decrease of 26.7 percent.

to show how long the disease has been in progress. Not one physician in five, to be sure, fills in this space and the health authorities have not thought it worth tabulating. Hence in order to get the 3,095 random cases used in section A under New York it was necessary to wade through fifteen or twenty thousand cards.

The rest of Table 5 indicates that during the epidemic at New York the following conditions prevailed: (1) When the temperature rose, not only the onset of influenza, but also the deaths from both influenza and pneumonia increased notably; (2) When the temperature was stationary, the rate of onset rose somewhat, while the deathrate changed but little; (3) When the temperature dropped both the rate of onset and the deathrate diminished greatly. This does not mean that low temperature is favorable, but merely that a *drop* gives a healthful stimulus. If the temperature stays low it becomes harmful. In Boston the effect of variability on the epidemic was the same as in New York except that the deaths from influenzza depart somewhat from the rule and diminish when the temperature rose as well as when it fell.

Taken as a whole Table 5 is surprising. In spite of the suddenness with which the epidemic fell upon the country without apparent regard to the weather, six sets of data out of seven show precisely the same relation to variability as do the 400,000 deaths from disease in general during the 8 years described above. The seventh set shows a slightly different relation like that of deaths from both kinds of pneumonia under normal conditions as given in Table 3. All alike, however, indicate unequivocally that a drop in temperature is favorable, even though a continuance of low temperature does harm. Moreover, in the great majority of cases the combined effect of marked variations of temperature in both directions is better than the effect of uniformity. This would apparently be true in all cases were it not for the almost universal overheating of houses which goes to great extremes when the outdoor temperature is rising. In view of all these facts it seems reasonable to conclude that even in the throes of the worst epidemic the severity of the disease might be reduced appreciably by creating within our houses the mildly variable and fairly low temperatures which prevail when the outside air is growing cooler.

12. Effect of Humidity in Mitigating the Epidemic

Turning now to humidity, Table 6 shows that in New York City the lower the humidity the greater the number of cases of influenza and the greater the number of deaths from both influenza and pneumonia. The importance of moisture appears to be even greater than that of variability. At Boston, however, there is no such regularity. In general, as appears in the averages, the dry days are unfavorable, those with a moderate degree of humidity are on the whole the best, and the very moist days intermediate. Possibly this means that the damp east winds of Boston introduce a complicating factor which is not present in New York. In studying operations at Boston, the damp days appeared to be decidedly the most favorable for the operation, but a few days later, the days with a moderate humidity of 60 to 65 percent and a temperature of 65° were the best, while the dampest days were not so good. Extreme dryness was always the worst condition. It is quite possible, however, that in Boston the sudden onslaught of the influenza epidemic during a few days which happened to have a high relative humidity has masked the relationship which is so noticeable in the New York epidemic and also in ordinary pneumonia according both to Greenberg's studies and to the figures already given in this article. However that may be, it is noteworthy that low humidity appears in general to have a decidedly bad effect which is particularly marked in influenza. Thus with humidity, as with variability we find a relationship between the weather and the deathrate even in the midst of an epidemic. In spite of all the statements to the contrary, the virulence of epidemic influenza appears to be closely dependent on the weather.

TABLE 6. *Influenza and pneumonia compared with relative humidity*
(Figures in parenthesis show number of days)

	Rel. Hum. 0–55%	Rel. Hum. 56–80%	Rel. Hum. 81–100%
1. *New York.*			
A. Daily onset of influenza	16.8 (34)	− 5.9 (42)	− 9.9 (18)
B.			
C. Daily deaths from influenza	47.8 (24)	−14.6 (33)	−57.0 (13)
D. Daily deaths from pneumonia	38.0 (25)	− 8.1 (34)	−48.2 (13)
Average	34.2	− 9.5	−38.4
2. *Boston.*			
A. Daily reports of influenza	1.3 (44)	5.3 (93)	−10.5 (56)
B. Daily reports of pneumonia	1.9 (47)	− 6.1 (104)	9.1 (62)
C. Daily deaths from influenza	45.0 (54)	−21.0 (111)	0.0 (69)
D. Daily deaths from pneumonia	−19.8 (54)	9.5 (112)	13.2 (69)
Average	7.1	− 3.1	3.0

13. THE IDEAL THERAPEUTIC CONDITION OF THE AIR.

The facts given in this article seem to indicate that proper air is of the greatest importance not only in ordinary influenza and pneumonia, but in the epidemic forms. Presumably the same is true of tuberculosis and other respiratory diseases, hence, the ideal method of restoring health in such ailments and of preventing their occurrence would seem to be to have the air (1) *variable in temperature,* (2) *fairly moist,* and (3) *not too warm.* The best way to appreciate the ideal along all of these lines is to consider a day in the spring or fall when the thermometer ranges from perhaps 58° at sunrise to 70° at noon, and when the air is moist enough to cause heavy dew at night, but is fairly dry at noon so that the average humidity for day and night together is about 80 percent. On such a day people can be comfortable either indoors with the windows wide open or outdoors. Little variations of temperature occur constantly, not only because of the changes due to the heating of the earth by the sun, but because a little breeze stirs the air, a cloud obscures the sun for ten or fifteen minutes, or a person passes from the sunlight to the shade.

Contrast this ideal condition with that of the ordinary house, office, or sickroom. Throughout the time when the furnace is running the windows are kept shut practically all the time except perhaps for a morning airing, the great aim being to keep the temperature not lower than 68° or more often 70°. The humidity is always low, dropping sometimes to 15 or 20 percent and rising as high as 60 percent only on the rarest days. When the outside air is damp, which usually means that it is also warm, the good effect of a sufficient supply of vapor is largely destroyed by keeping the windows shut and thus letting the rooms become too warm. The one time when conditions approach closely to the ideal is after a storm when the air is still fairly moist but does not contain the condensed vapor that makes things feel clammy, and when the temperature is falling in such a way that the thermometer inside the house keeps dropping and then rising as the furnace fire catches up with the outside change. Those are the days when few people contract influenza and other respiratory diseases, and when few die from them. The science of engineering has progressed sufficiently to give us any kind of air and any degree of change and humidity.[9] The question is simply whether physicians can make their patients, and especially those who nurse the patients, realize the tremendous benefit of air like that which makes October and May the healthiest times of the year. The hospital and the sickroom are the places for insisting on a reform which must some day spread to all parts of the community and which will do much to eradicate the respiratory diseases.

14. Fluctuations in Bacterial Activity

Coordinate with the variations in man's health in response to the environment there are great fluctuations in the activity of the bacteria of influenza. The origin of these fluctuations is one of the most important problems of biology. Rhythms or cycles of one kind and another prevail in many organisms. For example, Woodruff[10] has shown that in the infusorian known as paramoecium the rate of a sexual reproduction is subject to marked rhythms or cycles ranging in length from about 10 to 60 days. At the lowest point in the cycle there occurs a peculiar rearrangement of the cell structure, "endomixis." Although this is not sexual in any respect, since it concerns only a single cell, it seems to serve as a stimulant analagous to conjugation. Its occurrence is almost invariably followed by a marked increase in the rate of reproduction, as if the cells had been revivified. Then, after a decided maximum has been attained the stimulus wears off, and the reproductive rate again falls to a low ebb, after which a recurrence of endomixis initiates a new cycle.

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[9] For a discussion of the practical methods of accomplishing this see an article in The Modern Hospital, Chicago, April and May, 1920, entitled "The Purpose and Methods of Air Control in Hospitals."

[10] Woodruff, L. L., "Rhythms and endomixis in various races of *Paramoecium aurelia*," Biol. Bull. 33: pp. 51–56, 1917.

"The influence of general environmental conditions on the periodicity of endomixis in *Paramoecium aurelia*," Biol. Bull. 33: pp. 437–462, 1917.

The most striking feature of endomixis is the fact that it occurs simultaneously in unrelated races of paramoecium even when they are kept under markedly different conditions of temperature and nutrition. At the beginning of an experiment when the environmental conditions usually suffer a sudden change, the process is often hastened a little, thus showing that environment has something to do with the matter. Thereafter, however, all races or strains, no matter what their origin or their thermal and nutritional environment, fall into the same irregular cycles. One strain may be reproducing faster than another so that the number of generations from endomixis to endomixis may be different, but the *time* interval is the same for all strains. This suggests that an unknown factor of the environment is at work. Occasionally a strain fails to show endomixis when the process occurs in other strains, but the invariable result is death within a short time. Thus the revivifying internal rearrangement of the cells through endomixis seems to be essential to continued asexual reproduction of paramoecium. This simple animal has been found typical of life in general in so many and such important respects that we may well suspect it of being typical in this also.

If the endomixis of paramoecium really represents a widespread vital process, the cause of the cycles is of extreme importance. Among other things it may open the way to an understanding of the increase in virulence and presumably in the rate of reproduction, which characterizes certain types of bacteria during epidemics. Woodruff's work seems to demonstrate clearly that although nutrition and temperature cause marked cycles of their own, they are not the cause of the endomictic cycles now under consideration. This naturally raises the question whether or not the cycles are an innate function of life independent of environment. Their synchronism under highly varying conditions of temperature and nutrition seems against this. Moreover, the environmental causes are by no means exhausted. For example, far too little attention has been paid to atmospheric electricity. Over a decade ago Stone[11] showed conclusively that even a single spark or a very weak galvanic current in the nutrient media of bacteria, yeast, and other plants produces a marked acceleration in the rate of reproduction. A positive charge is more effective than a negative; too great a charge reduces vitality; and the right charge may increase the rate of reproduction a hundred-fold. We are led to inquire whether endomixis and its consequent cycles may not be partly due to electrical changes in the air. Such changes are well known. Everyone has seen electric sparks shooting from a cat's fur, from his own clothing, or from other sources. Before a thunderstorm, or while a snowstorm is brewing there are peculiar electrical conditions which change completely as soon as the storm breaks. Such conditions, acting either directly upon the nervous system or indirectly by stimulating the bacteria within the human body may be the cause of the headaches and general oppression which many people feel just before a storm. So subtle are the electrical conditions that they are able to penetrate the human body or to be effective within a thermostat. Thus in electricity we have an agency which is constantly varying and which has been proven experimentally to cause a remarkable stimulation of reproductive activity in bacteria and many other forms of life. Few phases of ecology offer a more fruitful field of study than endomixis and other cyclical phenomena on the one hand, and the effects of the less known environmental conditions such as electricity on the other.

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[11] Stone, Geo. E., "Influence of Electricity in microorganisms," Bot. Gaz. vol. 48, pp. 359–379, 1919.

Let us apply the foregoing reasoning to epidemics, especially to influenza. On a large scale an epidemic seems to represent the same thing that Woodruff's endomictic cycles and Stone's periods of electrical stimulation represent on a small scale. In both cases a single stimulus sometimes seems to increase the reproductive power of the paramoecia and bacteria for months. An epidemic may merely represent a similar increase in certain bacteria which cause disease. Suppose a bacterial form is residing in the throat. Its environment comprises chiefly three kinds of conditions: chemical, thermal, and electrical. All three may be altered by the condition of the air, for if dry cold air, for example, is inhaled it not only causes a slight reduction in the surface temperature of the throat, but by its drying action it may change the chemical environment. If this alters the relative rate of reproduction among the bacterial flora a further chemical change ensues. Suppose now that when a certain species of bacteria is favored by ideal conditions in the thermal and physico-chemical environment, it also receives an electrical stimulus or undergoes a process like endomixis under some other environmental control. In that case there will be a sudden increase in the rate of reproduction. This increased rate may last for months and thus produce an epidemic.

Another consideration may explain the occasional occurrence of epidemics of extraordinary virulence such as that of 1918. There is still much doubt as to just what form of bacteria causes influenza. This probably means that the disease is due to several bacteria, each contributing its own special disability. If such is the case, the most stimulating conditions for the various kinds are presumably different. Suppose that in quick succession there occur such environmental conditions that all the types of bacteria are stimulated. Then there will be an epidemic of unprecedented proportions. When all the types are at the height of their activity, the disease will assume the most virulent form. As it subsided the relative importance of different bacteria will vary and we shall have various forms of the disease. So, too, as the bacteria migrate from place to place the environmental conditions may stimulate or retard one or another type of bacteria with corresponding modifications in the disease.

All this is avowedly speculation, but it is controlled speculation. We are looking forward toward a future in which the science of ecology shall make its proper contribution to human welfare. Hence we must survey the whole field and must boldly project our ideas as far forward as possible. Searching on this side and on that by means of speculation and then by means of experiment, we may light upon principles which will revolutionize many phases of man's activity. In the realm of health there are clearly two great things to be done; one is to determine the optimum for mankind in respect to all the various features of the environment; the other is to determine in the same way the optimum for harmful bacteria. When that is done we can create the conditions that favor man, and destroy those that favor the bacteria. In this great work there is a part for every ecologist to play, whether he deals with plants, animals, or man; for what we now need most is a determination of the great principles on which the science is founded.

15. SUMMARY

1. The condition of the air has an important bearing on the diseases of the respiratory system. This paper presents an analysis of the relation between atmospheric conditions and the diseases of pneumonia and influenza in order to determine what conditions are best for patients suffering from these diseases.

2. Aside from epidemics, the deathrate from influenza as well as that from pneumonia, varies inversely with temperature: influenza begins with the frost, becomes severe when the temperature averages below freezing, reaches a maximum when the weather is coldest, and then declines.

3. Considering the daily deaths from pneumonia in relation to temperature and humidity, it is found that the deathrate from lobar pneumonia in New York City from April, 1917, to March, 1918, is less when the humidity is higher than when it is low. This applies to each of the eight temperature groups into which the year has been divided. At high temperatures the advantage of high humidity is less, and probably both extremely high and extremely low humidities are harmful. In bronchial pneumonia the effect of humidity appears to be less marked than in lobar pneumonia, although high relative humidity still shows an advantage over low humidity. Most significant is the fact that for outdoor temperatures of between 55° and 70° Fahrenheit the deathrate from lobar pneumonia remains at a rather uniform and comparatively low level so long as the relative humidity is not below 65 percent, but a drop of 20 percent from this humidity increases the deathrate

by at least one third. Much of the harm attributed to cold weather is probably due to injuriously low humidity in hospitals and houses. Data for influenza in relation to humidity are lacking, but since the deaths from influenza follow closely those from lobar pneumonia, it is probable that the relation is similar.

4. Variations in temperature cause a decrease in the deathrate from pneumonia. A drop in temperature, as distinguished from steady cold, is more favorable than a rise. Both a rise and a fall are more favorable than uniform temperature. Other data indicate that the health of Americans and Europeans is best with an average day and night temperature of 64° F. and relative humidity of 80 percent. The human body seems to have a decided optimum of temperature, humidity, and variability, and to be highly sensitive to any departure from this optimum.

5. Data on the influenza epidemic of 1918 also show that marked variations in temperature in both directions are more favorable than uniformity. The figures for New York show that the lower the humidity the greater the number of cases and deaths from influenza and pneumonia. In Boston extreme humidity, possibly due to damp east winds, is injurious.

6. The ideal air is (1) *variable in temperature,* (2) *fairly moist,* and (3) *not too warm,* air like that which makes October and May the healthiest time of year.

7. Man's health varies not only in response to the environment but with fluctuations in bacterial activity due to rhythms or cycles. Woodruff has found cycles of from 10 to 60 days in the infusorian paramoecium. A rearrangement of the cell structure, endomixis, increases the rate of asexual reproduction and initiates a cycle. Endomixis occurs simultaneously in various races of paramoecium, even when they are kept under different conditions of temperature and nutrition. The cause of endomixis is unknown, but it is suggested that atmospheric electricity may play an important part. Epidemics seem to represent the same thing as endomictic cycles and electric stimulation.

8. Further ecological work is required to determine (1) the optimum environment for mankind, and (2) the optimum for harmful bacteria.

EVIDENCE OF CLIMATIC EFFECTS IN THE ANNUAL RINGS OF TREES[1]

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The first substantial comparison between rings and rain with which the author is acquainted was made by the astronomer, J. C. Kapteyn of Holland, in 1880 and 1881 on oaks in the Rhine region. Professor Kapteyn has recently prepared and published a brief pamphlet on the subject.[2] A similar comparison between the growth of the great sequoia (*Sequoia gigantea*), and rainfall is shown in figure 1 in which the curve for rainfall is from Huntington,[3] from data at Fresno, 70 miles away and 5,000 feet lower in elevation. In spite of widely different conditions there is evident resemblance at a number of places in this comparison. It is a great pity that no proper records can be obtained in the actual region of the sequoias nor are any but the most superficial observations being made at the present time.

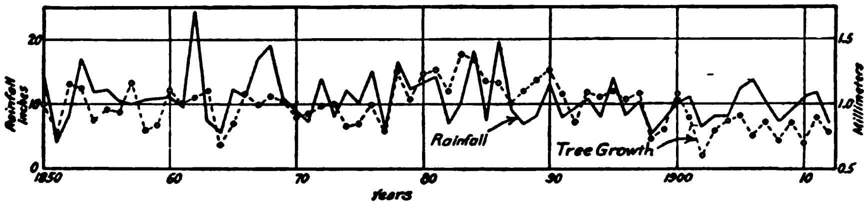

FIG. 1. Comparison of rainfall at Fresno, California, and growth of sequoias. (Rainfall after Huntington.)

The material here presented has emerged in the process of dating and measuring about 85,000 annual rings which had grown in some 275 different trees in the states of Oregon, California, Arizona, Colorado, and Vermont, as well as in England, Norway, Sweden, Germany, and Bohemia. The climatic evidence is of three kinds, of which the first is shown in figure 2. This is the direct correlation between the annual rings of yellow pine (*Pinus ponderosa*) and the rainfall at Prescott, Arizona. The trees grew within one mile of the location of the weather records. Although the curve is based on only 10 trees, its accuracy is over-abundantly checked by nearly a hundred trees at greater distances. The upper pair of curves representing the original values shows a very substantial agreement. In the lower pair of curves a simple conservation formula has been applied, producing a more marked agreement. The corrected values of tree growth represent the rainfall with an accuracy of about 85 percent. These pines grow at as low, and therefore at as dry an elevation as they can survive. Their rings show certain characters which seem to be dependent on the way in which the precipitation is distributed throughout the year. Much material along this line has been accumulated, and, when it is worked out will certainly increase the accuracy with which these trees represent the local rainfall.

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[1] Presented before the St. Louis meeting of the Ecological Society of America, January, 1920.

[2] Kapteyn, J. C., "The growth and meteorological factors," Rec. Trav. Bot. Neerland 11:70, 1914. Kapteyn found growth cycles of 12.4 years, being the same in different species.

[3] Huntington, Ellsworth, "The Climatic factor as illustrated in Arid America," 341 pp., plates and maps, Carnegie Inst. of Wash. Publ. 192, 1914.

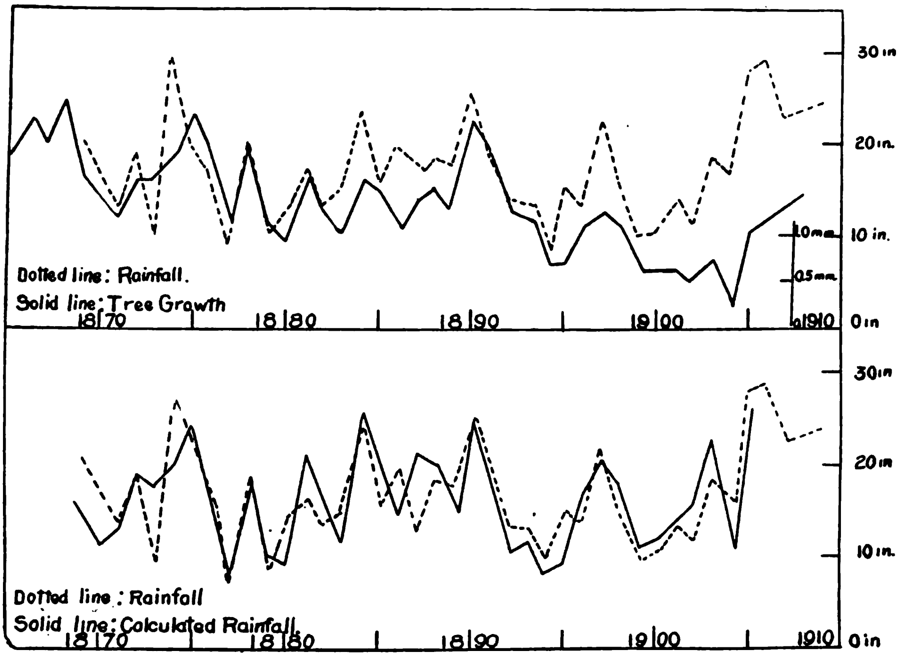

FIG. 2. Comparison of forty-three years of rainfall and tree growth at Prescott, Arizona.

The second form of evidence is the marked resemblance found in certain individual rings over a wide extent of the country in which climate is the only common factor. This is illustrated in figure 3 showing the years 1840 to 1864 in western trees. There are many points of resemblance and some interesting points of difference, but the figure is arranged especially to show the small ring for 1851. The three sequoias at the top cover 50 miles in California. Then there is a gap of 450 miles to the yellow pines of Arizona.

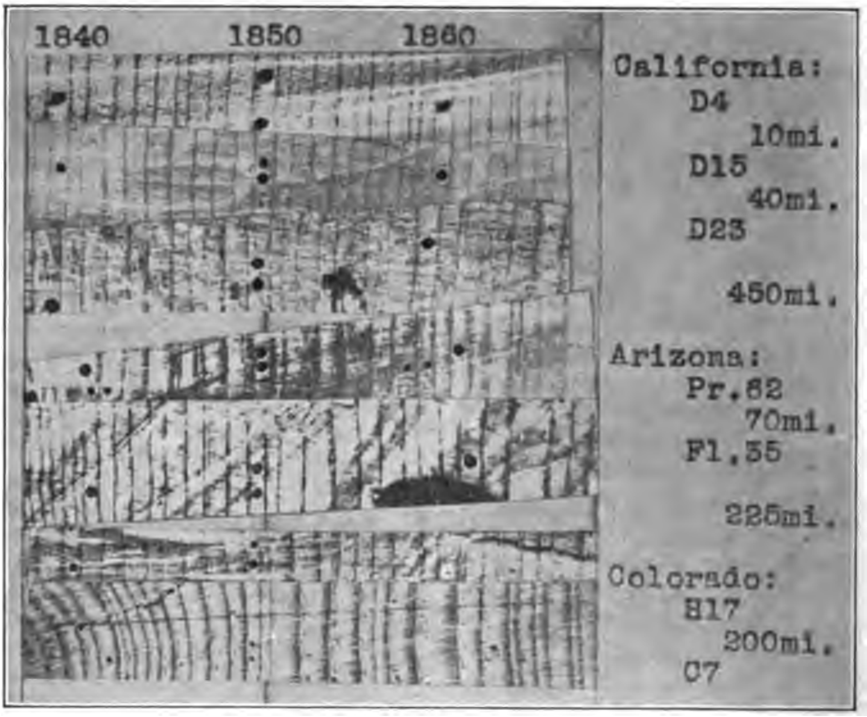

FIG. 3. Similarity in the ring of 1851 and others across 750 miles of country.

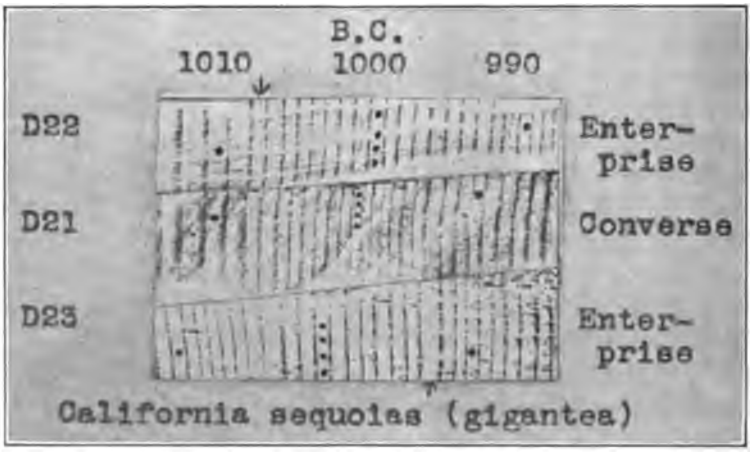

FIG. 4. Similarity in young sequoias across fifty miles of country. Note especially the rings for the years 993 and 1008 B.C.

Here two individuals 70 miles apart are given. Two hundred and twenty-five miles to the northeast a yellow pine in southwestern Colorado shows the same effect, checked by a Douglas fir from Pikes Peak, 200 miles beyond. The distance in an air line covered by these trees is 750 miles.

The great age of the sequoias enables us to make comparisons of conditions that existed two milleniums ago. Figure 4 shows rings which grew near the year 1000 B.C. In the center is shown a tree north of the General Grant National Park, while above and below are the same years in two trees south of the Sequoia National Park and 50 miles distant. Sequoias are less sensitive in their early years and do not show differences as clearly, but the ring dated 993 B.C. was very large, especially in the lower two sections, and the one dated 1008 B.C. was small, especially in the upper two. We cannot as yet go much earlier than that since the earliest complete rings in the oldest three trees so far found, are respectively 1087 B.C., 1122 B.C., and 1305 B.C. Figure 5 shows the center of the oldest; at the extreme point is a portion of the ring which was formed in 1306 B.C. The dating of those ancient rings has been a process very far from mere ring counting, for unchecked counting in these old trees (and many others) is very treacherous. These dates have meant the study of nearly 55,000 different rings and repeated minute comparison of those for each year as found in the 35 different

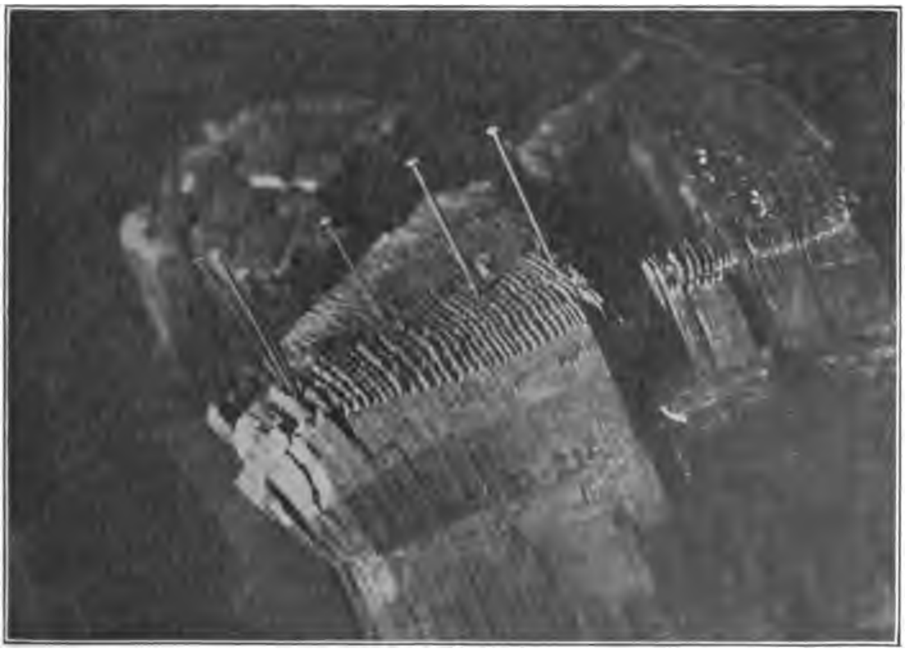

FIG. 5. Centre of oldest sequoia showing ring of 1305 and part of that of 1306 B.C.

trees. This has taken years of time and several trips to the sequoia forests. In this way omissions and errors were discovered and verified. Thus it is hoped that errors in dating these very interesting trees are very small or altogether absent.

The third type of climatic evidence is really an extension of the one just described. But instead of merely taking into account similarities in individual rings, it uses similarity in ring variation over large areas. This is done by a form of harmonic analysis for which I have constructed an instrument called a periodograph capable of analyzing plotted curves into their component cycles, if such exist.

Figure 6 presents the analysis of the sequoias and yellow pines. The various possible periods in years are marked at the tops and bottom; dates are at the left. The various short vertical lines show the duration of the respective cycles found. The last 500 years of the sequoia analysis fall just below the black line, and at the bottom is the analysis of the same period in the yellow pines. Though 450 miles separate these two groups there is considerable resemblance between them. Similar periods occur at 25 years, 23.9, 20.0, 18.9, 17.7, 14.1, 12.7, 11.6, 10.7, 7.4 and 5.8 years with varying intensities. The sequoia alone shows a period at 21.6 and the pines alone show one at 15.7 years. The strong one in each at 11.6 is the well known

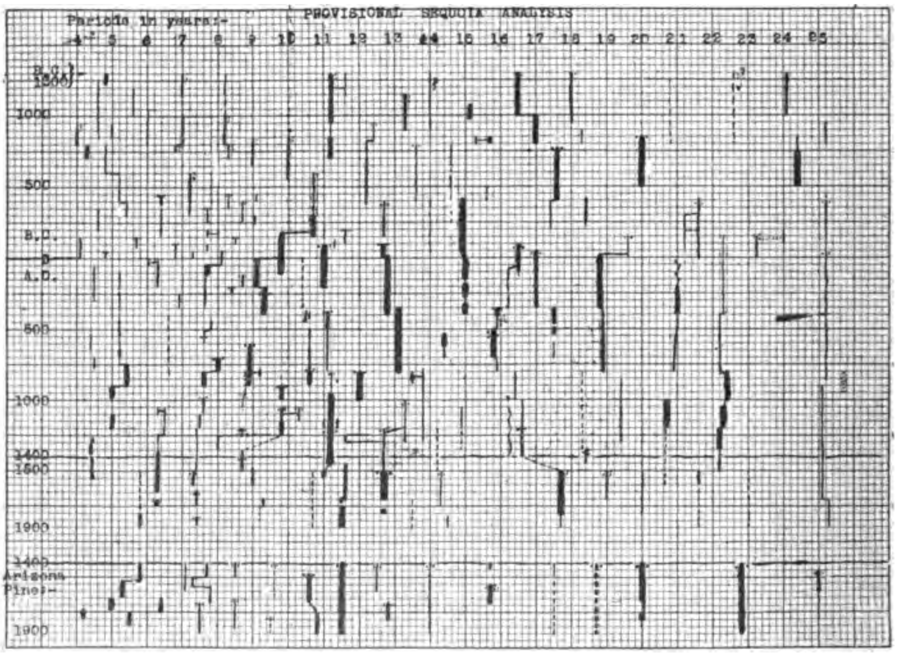

FIG. 6. Short period cycles in sequoia and yellow pine.

sunspot period. It is interesting to note that the only part of the sequoia with which the pine analysis shows good agreement is just where it should be, namely in the last 500 years. This evidence encourages one to believe in the reality of this kind of analysis and at the same time to regard climate as a very important if not controlling factor. This analytical method is entirely new but seems very promising.

In order to improve this analysis I am trying at the present time to produce from the 35 sequoias now represented in my laboratory collection, the best possible record of sequoia growth for 3,200 years. This means selecting the best parts of the best trees. The parts wanted of course are those which respond most closely to climatic influence. For this purpose I have proposed and am testing out a certain characteristic in the trees which I have called mean sensitivity. This may be described as the difference between each two successive rings divided by their mean. The quotients are arranged in groups of ten or some other number of years, and listed as the mean sensitivity of that period. Figure 7 shows the appearance of rings of different sensitivity. The first section came from a sequoia which grew in a swampy basin about 15 miles east of the General Grant National Park. The tree has a "complacent" growth, with rings all of nearly the same size. Its mean sensitivity is .11. The second is a sensitive sequoia which grew high up on the mountain side with a limited water supply and depended

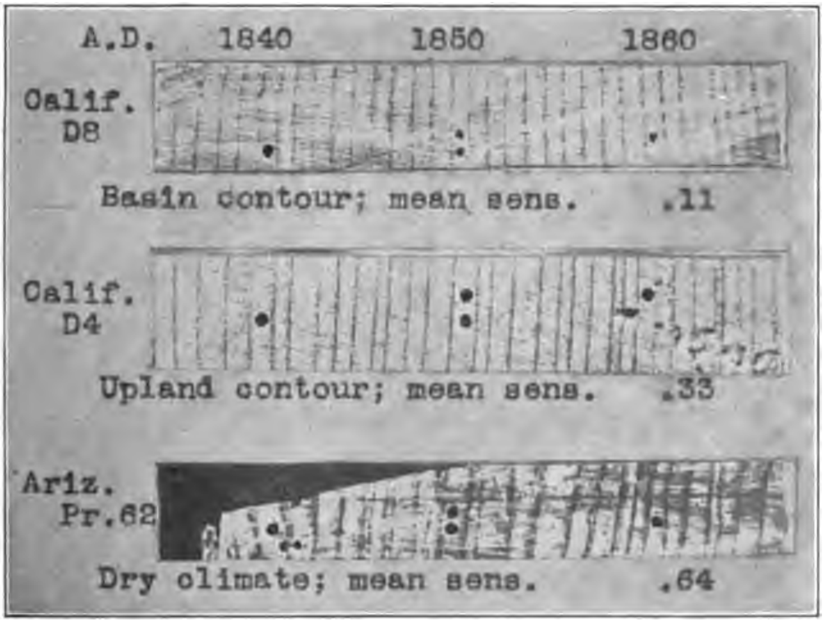
A.D. 1840 1850 1860
Calif. D8
Basin contour; mean sens. .11
Calif. D4
Upland contour; mean sens. .33
Ariz. Pr.62
Dry climate; mean sens. .64

FIG. 7. Appearance of rings showing different degrees of sensitivity.

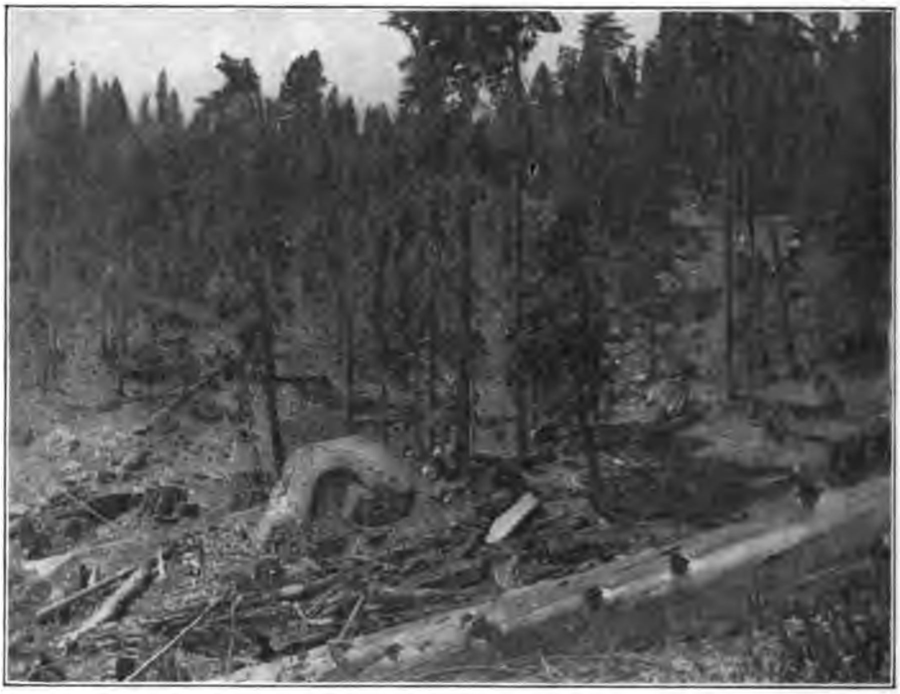

FIG. 8. Forest on moist uplands with little or no running water; the site of sequoias of good sensitivity (see Fig. 10).

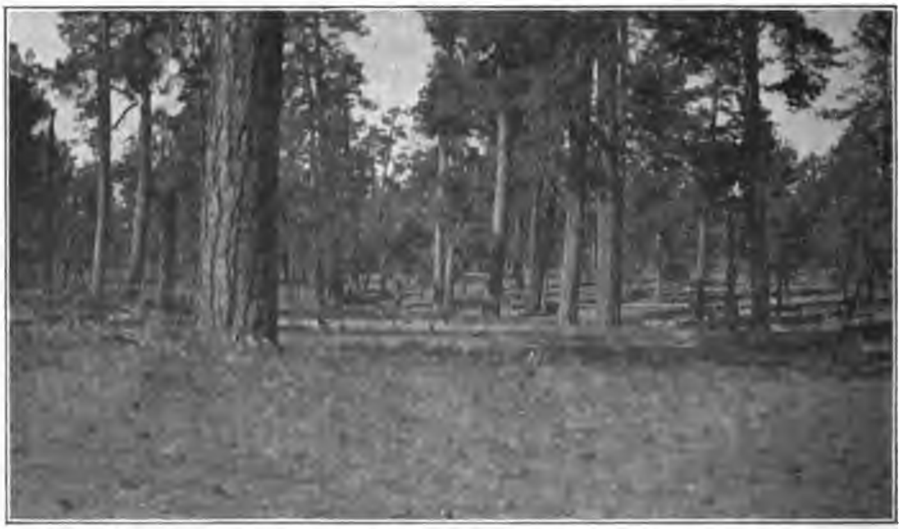

FIG. 9. Dry climate forest of western yellow pine in northern Arizona; site of trees of high sensitivity (see Fig. 10).

much more on the moisture of each year as it came. Its rings have more character and individuality, and the changes from ring to ring are much more evident. The mean sensitivity is .33. The third is a hyper-sensitive dry climate yellow pine near Prescott, one of the 10 used in the curves of Prescott tree growth already described. It grew near the lowest limit of the yellow pine. Some of its rings, such as 1841 and 1857, are so small as to be found with difficulty. Its variations from year to year are extremely large, and its mean sensitivity is .64. The character of the sites of the last two trees may be seen in figures 8 and 9. Figure 8 shows the site of the sensitive sequoia, in the moist uplands. The sample given is from the high stump in the left foreground. This location is about 800 feet higher in elevation than that of the tree with low sensitivity, and is near the top of the mountain. There is a small spring higher up and a small trickle of water near this tree, but, with the other trees near it, it shows a greatly increased sensitivity. Figure 9 is a typical view in the yellow pine forest in the dry climate of northern Arizona. One notices the isolation of the trees and the lack of competing vegetation so that the trees' chief struggle is against the dryness of the climate.

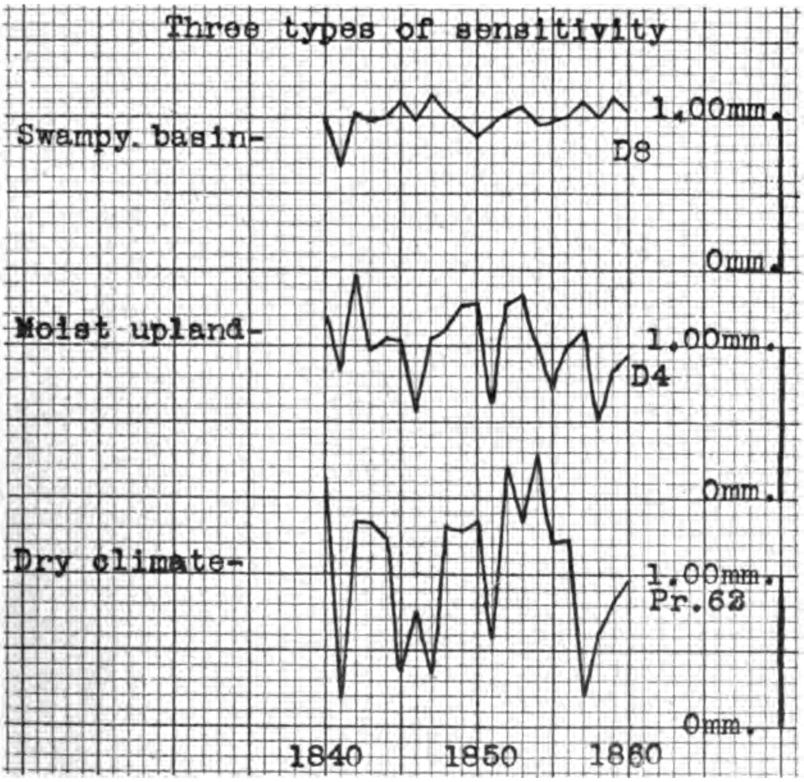

Fig. 10. Curves illustrating different sensitivity.

The way these variations in sensitiousness look in plotted curves is shown in figure 10 in which the curves of growth of these three trees show percentage departures, each from its own mean. The different character resulting from the different environment is at once apparent to the eye.

In conclusion I would say:

1. Trees probably integrate, and may be made to disclose to us, climatic combinations advantageous to certain types of vegetation.
2. The study of this subject promises to enable us to outline what might be called agro-meteorological districts, that is areas over which exist similar advantageous combinations of weather elements.
3. The application of the criterion of mean sensitivity promises to make possible the proper selection of sequoia records, which in turn will give us much climatic information about the last 3,200 years.
4. Information regarding suitable forests for similar study, located in central and other parts of North America, will be greatly appreciated by the writer.

[*Note.*—The foregoing paper presents an entirely new viewpoint toward the relation between climate and tree growth in that it recognizes that factors other than the seasonal rainfall influence the size of the trees' annual rings. Dr. Douglass' development of the idea of "mean sensitivity" represents a marked step forward in this important line of research. Foresters have been a little skeptical of direct correlations between climate and annual rings because their work has thrown them into direct contact with the intricacies of tree growth. In the forests of humid regions competition for light seems to play a more important part than variations in precipitation from year to year. A crowded tree will have smaller rings in a favorable season than a dominant tree in a poor season. Nevertheless, even in such forests it should be possible, with knowledge and care, to learn something of the past climate from tree rings. For example, in red spruce (*Picea rubens*) the period of suppression is indicated by an inner core of very narrow rings. If this period, and the later period of semi-suppression, is rejected the study of the dominant period should afford fairly reliable results. The difficulty is of course to decide what to use and what to reject. We believe that this difficulty is not insuperable. Even trees in the forests of semi-arid regions, such as the western yellow pine of the southwest, are not entirely free from crowding because they tend to grow in groups. Here, however, the problem is less difficult because yellow pine requires light and does not persist long in shade. As a general rule it would probably be fairly safe to say that the more light demanding the tree, the easier and safer will be the correlation with climated. EDITOR.]

POSSIBLE EFFECT OF SEASONAL AND LABORATORY CONDITIONS ON THE BEHAVIOR OF THE COPEPOD ACARTIA TONSA, AND THE BEARING OF THIS ON THE QUESTION OF DIURNAL MIGRATION

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There are reported here some new facts regarding the behavior of a species of marine copepod, *Acartia tonsa*. The writer has previously discussed the behavior of this organism in papers that deal with the possible relation of reactions to the habit of diurnal migration (Esterly, 1917*a*, 1919), the observations for which were made at La Jolla during the summer and fall of 1916; the animals were obtained either at the surface during the night or in deep water during the day. Such surface animals are positively phototropic when observed the next day, and are negatively geotropic in the light and positively geotropic in the dark. The specimens from deep water are negatively phototropic and positively geotropic in light and in darkness soon after they have been brought into the laboratory. The reactions of animals from the surface were noted only after the specimens had been in the laboratory for several hours because they were not to be obtained at the surface during the day and so the collecting was done at night. The possibility surely exists, therefore, that the behavior shown by animals hours after their capture may have been different in significant respects from that which would have appeared soon after their removal from the sea.

This possibility is made almost a certainty by observations obtained during the summer of 1919, when *Acartia tonsa* was taken in fairly large numbers in the morning and afternoon. The collecting was done by means of an open plankton net with a bottle tied into the peak. The specimens were taken to the laboratory right away and observations were begun at once.

When a collection is put into a dish standing before a window some of the animals are soon to be found on the side away from the window while a larger number are found on the side toward the window. The animals that I worked with during 1916 did not show that kind of distribution, at least not at the time that I used them; all were to be found on the window side of the aquarium. All or nearly all of the animals in the 1919 collections finally gathered on the side toward the light if the dish was left in front of the window for several hours, though at first there were the two well-defined portions.

As might be expected, the animals from the window side do not react to light as do those from the room side of the stock dish. The former swim toward the light while the latter swim away from the light. A shallow circular dish 16 cm. in diameter was used in a dark room to which daylight was admitted through a window 50 by 40 cm. A circle drawn on the bottom of the dish near the edge was marked off into divisions of about 15° each. The dish was placed so that one diameter was perpendicular to the window, the end nearer the window being called 90°, the opposite one 270°. The diameter parallel to the plane of the window was called 0°–180°. The center of the dish was set one meter from the window pane and animals were released one at a time from a pipette held over the middle point of the dish. When an *Acartia tonsa* swims it usually moves in a direct line without wandering around; this makes it possible to note the path taken by means of the degree marks on the circle near the edge of the dish. If an animal crossed the circle at 90° it means that it swam toward the light directly, while crossing at 270° indicates that it moved directly away from the light.

The following are examples of the behavior of specimens under the conditions mentioned above. Ten specimens from the window side of the stock dish were each tested once and they crossed the circle at these points: 35°, 100°, 90°, 105°, 45°, 85°, 90°, 90°, 90°, 75°. The paths of the first and fifth individuals diverged a good deal from a direct course toward the light, but the other animals swam toward the window. Ten other specimens in the same collection but taken from the room side of the dish crossed at: 150°, 75°, 275°, 50°, 50°, 100°, 275°, 275°, 265°, 280°. Four were positive and six were negative to the light from the window. On another day and with animals from another collection ten animals from the window side of the stock dish crossed the circle as follows: 90°, 90°, 90°, 90°, 215°, 90°, 90°, 90°, 90°, 90°—all but one moved toward the light; ten animals from the room side of the dish crossed at 270°, 225°, 270°, 75°, 90°, 270°, 260°, 260°, 275°, 270°—two moved toward the light and eight away from it. Ten specimens from the window side in a third collection crossed at 90°, 90°, 90°, 90°, 75°, 75°, 80°, 80°, 105°, 90°, 90°, all being positive. Seven individuals in a fourth collection and taken from the room side crossed at 320°, 315°, 285°, 270°, 330°, 260°, 300°—all were negative; fourteen specimens from the same collection from the window side were predominantly positive as shown by the points at which they crossed the circle: 285°, 220°, 75°, 105°, 105°, 105°, 120°, 220°, 270°, 120°, 90°, 90°, 100°, 70°.

In view of the data given above there is good reason for considering the animals that gather on the side toward the window as positively phototropic, while those on the opposite side are negative.

The conclusion from their behavior toward light that the *Acartiae* in a collection are of two sorts is strengthened by the behavior in a vertical container. For these observations the animals were put into flat bottom glass

TABLE I. *Geotropism of Acartia tonsa obtained at surface during the day. Distribution in diffuse light and darkness, given in A and B for successive hours of observation. Temperatures over 18° C. "R" means that the animals came from the room side of the stock dish; "W" means that they came from the window side. The former are negatively, the latter positively phototropic.*

Hour after capture	Whole no. of animals observed	Percentage distribution in the sections					No. of observations			Center of distr
		Top V	IV	III	II	Bot. I	Total	% showing more ans. in		
								Upper ½	Lower ½	
A. In the light										
R 1..........	488	7	4	5	6	78	81	4	95	1.5
W 1..........	532	69	5	3	3	20	82	81	17	4
R 2..........	356	25	9	5	6	55	19	28	69	2.5
W 2..........	393	78	4	2	4	12	70	93	6	4.3
R 3..........	89	36	6	4	9	45	16	44	44	2.8
W 3..........	166	86	5	1	—	8	30	90	3	4.6
R 4..........	159	44	8	3	9	36	26	54	42	3.1
W 4..........	52	94	—	2	—	4	11	91	—	4.8
R 5..........	289	47	8	7	6	32	55	56	35	3.2
W 5..........	318	87	4	2	1	6	63	95	5	4.7
R 6..........	189	61	9	4	5	21	36	72	19	3.8
W 6..........	240	84	6	3	2	5	48	94	7	4.6
R 7, 8........	199	63	5	2	3	27	38	63	37	3.7
W 7, 8........	85	76	13	2	3	6	17	100	—	4.5
R 9, 10, 11....	94	58	5	3	10	24	16	56	31	3.6
W 9, 10, 11....	72	82	4	–	—	14	15	93	—	4.3
B. In darkness										
R 1..........	329	9	7	5	3	76	65	5	89	1.9
W 1..........	519	46	9	4	4	37	99	54	38	3.2
R 2..........	186	12	9	7	1	71	38	21	76	1.9
W 2..........	349	46	8	4	5	37	69	49	46	2.6
R 3..........	57	25	16	–	5	54	11	36	45	2.5
W 3..........	165	68	7	2	1	22	32	88	12	4
R 4..........	105	30	17	9	15	29	22	36	36	3
W 4..........	43	58	7	5	7	23	9	78	22	3.7
R 5..........	240	48	12	6	2	32	47	62	21	3.4
W 5..........	278	64	6	5	4	21	54	85	11	3.8
R 6..........	173	45	11	4	6	34	35	54	31	3.1
W 6..........	222	57	9	6	6	22	46	72	11	3.7
R 7, 8........	127	42	15	8	1	34	24	44	17	3.2
W 7, 8........	75	72	8	3	5	12	13	87	12	4.2
R 9, 10, 11....	67	54	13	6	5	22	10	70	—	3.7
W 9, 10........	50	66	8	8	2	16	11	100	—	4
AFTER RETENTION OVERNIGHT IN THE LABORATORY										
C. In the light										
R 18–30......	620	73	7	5	4	11	130	87	3	4.3
W 18–30......	407	66	8	2	3	21	87	80	19	4
D. In darkness										
R 18–30......	665	52	9	7	6	26	139	70	17	3.6
W 18–30......	395	57	5	3	2	33	87	61	29	3.5

tubes 50 by 3 cm. The tubes were filled with clean sea water brought from off shore in glass jars. Five or six animals were put into a tube as soon as possible after the collection was obtained. The tubes were marked off into five sections of equal heights and the number of animals in each of the sections was noted from time to time. The distribution of animals from the two sides of the stock dish was compared both in darkness and in diffuse light. Usually a set of each sort was observed in diffuse light at the same time that similar sets were kept in darkness, so that the distribution in four tubes was noted at once. Most of the individuals were adult females but the behavior of the sexes is the same, so far as my observations go.

The accompanying table is arranged to show in summary the distribution of many sets of animals. The abundance in the different sections changes as the experiment is continued and the records are shown as they were taken hour by hour. In explanation of the terms used in the table it should be stated that "whole number of animals observed" is the sum of all the records of distribution in all the experiments within a given time and under given conditions. Each living animal was counted as many times as there were observations during any experiment. "Percentage distribution" is the proportion of the total number of animals observed in each section, for all experiments, to the whole number observed. "Number of observations" means the number of times the distribution was recorded. The "center of distribution" is the average position (as between top and bottom) of the whole number of animals. It is obtained by multiplying the total number of animals observed in each section by the number of the section, and dividing the sum of the products by the "whole number of animals observed." The centers are set down in units and tenths; the unit is considered to be the middle point of the section having the corresponding number. If one center is compared with another the difference between them, if any, is the magnitude of the shift of the whole population.

The difference in the behavior of animals from the window and room sides of an aquarium is plainly evident from the results given in the table. Through ten or eleven hours of continuous observation following the taking of the animals, when records were made several times an hour, there are noteworthy differences in distribution. When kept in diffuse light the positively phototropic animals (those from the window side) remain in the upper sections of the vertical tube (see the lines designated by "*W*" in part *A* of the table). Under the same conditions the negatively phototropic animals (from the room side) remain at lower levels though there is an ascent amounting to two sections of the tube during the first four or five hours (see lines designated by "*R*" in part *A* of the table).

The geotropism of negatively phototropic animals in darkness (part *B*) is practically the same as in the light: most of them when first put into the tube descend into the bottom section and ascend later. The center of distribution is in the second section from the bottom during the third hour and from that time on it is in the middle section (see the lines designated by "*R*" in part *B*). The positively phototropic animals (those from the window side) are found at higher levels than the others, as is shown by comparing the percentages and centers of "*R*" and "*W*" in part *B*. In that respect at least the behavior of positive animals ("*W*") in the light and in the dark is similar; although they descend farther in the dark than in the light and do not rise as high they are always at higher levels than "*R*" animals.

On the second day after they are obtained both sorts of animals are negatively geotropic, though more strongly so in the light (parts *C* and *D* of the table). There is practically no change hour by hour on the second day so that the summary of distribution is set down in parts *C* and *D*.

It is interesting to compare the data in the table above with the results obtained in 1916. The latter showed that surface animals were negatively geotropic in diffuse light and positive in the dark (Esterly, 1919, p. 20 and Table 1). It should be noted again that the animals came from the surface during the night and were left in the laboratory until the following day. In 1919, however, the animals could be taken at the surface during the day and were used immediately. Whether this difference in preliminary treatment accounts for the differences in behavior cannot be stated. But if retention in the laboratory accounts for the positive geotropism shown in the dark by the 1916 animals, it would seem that the same behavior could have been expected in 1919 also after holding the animals in the laboratory for hours. Yet this is not the case as may be seen in part *D* of the table; both sorts of animals ("*R*" and "*W*") are shown to be largely in the upper two fifths of the tube after they have been in the laboratory all night.

The animals observed in 1919 did not show the geotropic rhythm that was evident in 1916 (Esterly, 1917*a*). It was particularly desired to note that sort of behavior again, but it did not appear. The data in the table show that there is no particularly noteworthy change in the distribution either in the light or in the dark after about the fourth hour of observation; even on the second day the distribution is practically constant and about what it was beginning with the fifth hour on the first day.

The results given here, when considered in connection with those that appear in the other papers referred to, make one dubious as to how to apply them to the problem of diurnal migration. It may be well to glance at the experimental data in their relation to the behavior in nature. My papers have shown that two species of *Acartia* are negatively geotropic in diffuse light but positive in the dark (Esterly, 1917*a*; 1919, p. 20) when the specimens come from the surface, and that there is a rhythm in geotropism when the animals are kept in the dark that seems to duplicate on a small scale the vertical migration in the sea. The possible bearing of these results on the diurnal migration was discussed in another place (Esterly, 1919, p. 22) and it was stated that "the experiments do not show why animals obtained at the surface should not be found there during the day; indeed the laboratory results show that the species 'ought' to be at the surface during the day." The preceding statements make a brief summary of the results obtained in 1916.

In 1919, however, specimens of *Acartia tonsa* were abundant at the surface during the day and, as shown in this account of the experiments, some of the animals in a collection are positively phototropic and negatively geotropic from the first in diffuse light and (to a less extent) in the dark; while others, negatively phototropic, are at first positively geotropic in diffuse light and in darkness but later become negative.

Such discrepancies raise questions, and the first one that comes up is, What is the reason for the differences in behavior in 1919 as compared with 1916? Two answers may be suggested. It is possible that the two seasons differed to such a degree that the behavior in the sea as well as in the laboratory was altered. Whether there is anything in this suggestion or not can be ascertained, I believe, by a study of the field data obtained in 1916 and 1919 relating to the actual collections and also to the conditions of temperature, salinity and the like. The other possibility is that keeping the animals in the laboratory before beginning observation may account for the results obtained in 1916. I worked at that time on the assumption that retention in the laboratory "does not affect the behavior of animals that were obtained at the surface during the night" (Esterly, 1919, p. 18). But since the behavior of at least some of the animals taken at the surface during the day changes in a few hours the same would probably be true of animals obtained at night.

Another question that is important in this general connection is, Shall an observer apply to a problem in natural history only those experimental results obtained soon after the animals are taken from their natural surroundings, or is it desirable to wait until they have "become accustomed" to laboratory conditions? From one point of view it would seem to be better to use the results gained before the artificial conditions of the laboratory have affected the organisms any longer than necessary. On the other hand if the behavior immediately after capture differs from that shown later it may be for the reason that the animals were upset, so to speak, by removal from the sea, necessary handling and so on, and that they should have time to "settle down." It does not seem wise to attempt to fix any rule but it is plain that a student of behavior who desires to apply his results toward an interpretation of habits in nature should always look for a possible effect of laboratory conditions or something connected with laboratory procedure in modifying reactions. A more extended discussion of this matter has been given in another place (Esterly, 1919, p. 66).

If all the animals in a collecting bottle were negatively geotropic it would be comparatively easy to account for the presence of *Acartia* at the surface of the sea during the day. Some of the specimens are negatively geotropic and if this reaction takes place in the sea the organisms would be found at the surface in the light. But there are also numbers of animals whose vertical distribution in a tube does not correspond for several hours with their distribution in the sea when they were swept into the net. These representatives of the species cannot be disregarded simply because their laboratory reactions do not "fit" their behavior in nature. These specimens are as truly *Acartia tonsa* as those which are negatively geotropic from the first. If one happened to be observing animals that came from the room side of a stock dish the conclusion would be justified that *tonsa* is not found at the surface during the day.

In view of what has been said it seems proper to inquire whether the geotropism of *Acartia tonsa* as a species is to be called positive or negative. If based on experimental data the answer depends on the particular individuals observed, if the vertical distribution is noted as soon as possible after the collection is obtained. If the answer is based on the fact that specimens can be taken at the surface during the middle of a sunny day it could be said that the species is negatively geotropic. Yet the animals separate into two behavior classes in the laboratory, one being positive to horizontal light and remaining near the top of a column of water, the other being negative to light and at first positively geotropic. Because some specimens in the laboratory are negatively geotropic may it be assumed that the species at large has the same behavior? If such an assumption is made what shall be said about the positive geotropism of the other specimens that were obtained at the same time as those that remain at the top of a vertical tube? Such questions are difficult or impossible to answer at the present time, but it is important to call attention to them even if nothing else is done.

There has been much insistence in publications that deal with certain phases of the program of the Scripps Institution on the need of both experimental and field data for the solution of questions in natural history (Esterly, 1917*a*, 1917*b*, 1919; Michael, 1916). There is no need to go over this matter again here, but it is well to point out that the laboratory observations reported in this paper show facts about *Acartia* that field observations would not reveal. The plankton net could not sort the specimens that enter it into the two well marked behavior classes that appear in the laboratory. On the other hand it cannot be stated how the experimental facts are related to the vertical movement that appears to take place in the sea. The chief object in presenting the matters that have been discussed is to call attention to some considerations that must be kept in mind when it is desired to determine the relations between responses in the laboratory and habits in nature. There is no thought of suggesting that what is true of *Acartia* is necessarily true of other plankton forms, but it is likely that similar conditions will be found in other cases. At least it may be said that it is an open question how far reactions under experiment will reveal the reasons for behavior in nature, until the effect of laboratory conditions as such has been ascertained.

SUMMARY

1. Experiments made in 1916 with specimens of *Acartia tonsa* that were taken at night at the surface and left in the laboratory for several hours showed that all the animals were positively phototropic, negatively geotropic in the light and positively geotropic in the dark.

2. In 1919 it was possible to get specimens at the surface during the day and to observe their behavior within a few minutes. Some animals are positively and some negatively phototropic. The former have marked negative geotropism in the light; in the dark also they are negatively geotropic but to a less degree. The negatively phototropic animals at first show a pronounced positive geotropism which changes after three or four hours to a rather weak negative geotropism. Both sorts of animals continue to be negatively geotropic on the second day in light and in darkness, but the reaction is more pronounced in the light.

3. It is suggested that the differences noted in the two years (1916 and 1919) may be due to oceanic conditions or to alteration in the form of response during the time that the animals are kept in the laboratory. Whatever the explanation, the application of the experimental results to the diurnal migration problem is rendered difficult and uncertain.

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[*Note.*—The problem of the influence of laboratory conditions on plants and animals is becoming more and more pressing with the increasing need for exact experimentation. Although the problem may be more urgent in the case of animals than plants, still it applies to plants. For example a plant which has been grown in a greenhouse may be made to wilt, even when its roots are amply supplied with water, if placed in the open sunlight. This phenomenon is probably at the bottom of much confusion in the study of the wilting coefficient of soils. It is hoped that Professor Esterly's paper will stimulate further research along these important lines. EDITOR.]

A NOTE ON THE ECOLOGY OF HERONS

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The interrelations of living things are likely to remain for a long time the least understood of ecological problems. Their study often defies efforts at exactness or completeness, and "laboratory methods" are usually helpless. Yet these complex relations are far reaching and often of decisive importance. Darwin's famous and frequently quoted example of the effect of cats on the clover crop would seem to show that chains of cause and effect have rarely been recorded, and also that their importance is recognized.

A series of interrelations of this kind—from man to herons—recently came under my observation. The upper part of Belfast Lough in the North of Ireland is occupied by "the banks," an area of perhaps ten square miles, bare at low water but covered at high tide. This ground used to be very soft with shallow pools and anastomosing streams spreading over the dark oozy ground. At low water it was the feeding place of many birds. Curlews, sandpipers, redshanks, gulls, rooks and others were common; but by far the most conspicuous were the big herons (*Ardea cinerea*—closely allied to our *A. herodias*). These herons were always to be seen in some numbers, often very close to the railroad trains that passed their feeding grounds and to which they had become accustomed. Such was the condition thirty years ago.

Within recent years I have several times revisited this ground. Many birds are still there, some in undiminished numbers, but the herons are practically absent. On inquiry the following explanation was given to me and is borne out by my own observations. The only channel through the banks to the port of Belfast used to be through the shallow and meandering river Lagan. The city cut a straight and deep channel, about six miles long, from the port to deep water. Following this, in the course of a few years, the soft mud of the banks was replaced or covered by a firm sand, presumably due to a more direct tidal flow. As a consequence, great stretches of eelgrass (*Zostera marina*) disappeared, and with it the sand-eels and small fish which found shelter in it. The herons, thus deprived of their food, forsook their old haunts for the neighboring bays and loughs.

Thus the chain runs from man through the cutting of the channel, the extensive edaphic change, the eel-grass, the sand-eels to the herons.

PLANT DISTRIBUTION AROUND SALT MARSHES IN RELATION TO SOIL ACIDITY

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It is often denied that soil acidity has any particular relation to the distribution of plants; but as far as can be determined from their writings the majority of those who hold this view have either never made any determinations of soil acidity whatever, or have based such measurements as they have made upon misleading methods or unsound views as to the nature of soil acidity.[1] As a result of many hundreds of determinations of soil acidity and alkalinity made by the recently described method[2] upon plants growing under the widest possible range of physical and climatic conditions, the writer has found abundant evidence that the acidity of the soil is closely connected with the distribution of native plants. An account of a few observations is presented here, to illustrate the possibilities of this method in throwing light on the significance of peculiar types of plant distribution.

When a plant is described as characteristic of acid or of alkaline soil, it is not intended to imply that this is the only factor of importance in determining the place of growth, nor that the acid or alkali acts directly upon the plant. Some plants may *require*, for themselves or for symbiotic organisms, a soil of a definite acidity (or alkalinity); others may be favorably affected by some physical or chemical property of the soil which *accompanies* the development of that acidity; and still others may be *driven* into soils of a certain degree of acidity by more vigorous species which monopolize neighboring soils of greater or less acidities. The measurement of the actual soil acidities and alkalinities connected with certain species of plants, which is all that is attempted here, is but one step in the working out of the problem of why a given plant grows in a certain place. It is hoped that the results presented will indicate, however, the considerable, if not fundamental, importance of this often neglected step.

One of the most remarkable features of the vegetation of southern New Jersey, as pointed out by Stone,[3] is the presence of plants which are characteristic of the upland woods or meadows of the northern part of the State upon a strip of land extending southward along the coast, lying in part between the pine-barrens and the salt-marshes, and in part between the latter and the ocean. A list of twenty typical species showing this distribution, selected from those given by Stone, follows:[4]

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[1] It is planned to discuss the last statement in a subsequent paper.

[2] Journn. Wash. Acad. Sci., 10: 217. 1920.

[3] "The Plants of Southern New Jersey . . .," Ann Rept. N. J. State Mus. for 1910: 88. 1911.

LIST 1. PLANTS EXTENDING FROM NORTHERN UPLANDS SOUTH IN NEW JERSEY CHIEFLY ALONG THE COASTAL AREA

Wood reed-grass	(*Cinna arundinacea*)
Slender wild rye	(*Elymus striatus*)
Low cyperus	(*Cyperus diandrus*)
Woolly sedge	(*Carex lanuginosa*)
Starry false solomon's seal	(*Vagnera stellata*) (*Smilacina stellata*)
Wide-leaf ladies' tresses	(*Ibidium plantagineum*) (*Spiranthes lucida*)
American aspen	(*Populus tremuloides*)
Starry campion	(*Silene stellata*)
Spreading pearlwort	(*Sagina procumbens*)
Blunt-leaf sandwort	(*Arenaria* (*Moehringia*) *lateriflora*)
Columbine	(*Aquilegia canadensis*)
Lyre-leaf rock-cress	(*Arabis lyrata*)
American burnet	(*Sanguisorba canadensis*)
Swamp wild rose	(*Rosa virginiana* (*lucida*))
Hog peanut	(*Falcata comosa*) (*Amphicarpa monoica*)
Herb Robert	(*Geranium* (*Robertiella*) *Robertianum*)
Whorled milkwort	(*Polygala verticillata*)
Shrubby bittersweet	(*Celastrus scandens*)
Northern bugle-weed	(*Lycopus uniflorus*)
Pale wild sunflower	(*Helianthus giganteus*)

A few of the species of list 1 occur also in the marl area (Middle District) of southern New Jersey, but most of them are typical of the Piedmont or even the Appalachian mountain provinces further to the northwest, and do not enter southern New Jersey except along the coastal area. Many of those in the list have been studied by the writer in one or the other of these regions, and their soils have proved to exhibit on the whole circumneutral reactions: the reaction may reach a specific acidity of 10 or a similar specific alkalinity, but rarely lies farther than this from the neutral point.

More or less closely associated with these circumneutral soil species are found, in the coastal area, many plants which grow in southern New Jersey otherwise only in the pine-barren area, such as those in list 2.

LIST 2. PLANTS EXTENDING EASTWARD FROM THE PINE-BARRENS INTO THE NEW JERSEY COASTAL AREA, BUT ABSENT FROM OTHER AREAS

Brake	(*Pteridium latiusculum*) (*Pteris aquilinum*)
Larger pine-barren club-moss	(*Lycopodium adpressum* (*Chapmanii*))

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[4] The common names in this and the other lists are taken from Britton and Brown's "Illustrated Flora," with a few modifications; technical names are in accordance with the American code, but the synonymy is given in cases of recent changes which have not become generally accepted, and the names under the international code are likewise added.

Pitch pine	(*Pinus rigida*)
Panic grass	(*Panicum meridionale*)
Panic grass	(*Panicum oricola* (variety of preceding?))
Panic grass	(*Panicum lucidum*)
Pine-barren cyperus	(*Cyperus Torreyi*) (*Cyperus cylindricus*)
Twig-sedge	(*Cladium* (*Mariscus*) *mariscoides*)
Grass-leaf rush	(*Juncus aristulatus*)
Grass-pink orchid	(*Limodorum tuberosum*) (*Calopogon pulchellus*)
Early ladies' tresses	(*Ibidium vernale*) (*Spiranthes vernalis*)
Southern wild flax	(*Linum* (*Cathartolinum*) *floridanum*)
Inkberry	(*Ilex glabra*)
Sheep laurel	(*Kalmia angustifolia*)
Stagger-bush	(*Neopieris* (*Pieris*) *mariana*) (*Lyonia mariana*)
American cranberry	(*Vaccinium* (*Oxycoccus*) *macrocarpon*)
White thoroughwort	(*Eupatorium album*)
Blazing star	(*Lacinaria graminifolia* var.) (*Liatris graminifolia*)
Pine-barren goldenrod	(*Solidago fistulosa*)
Bushy aster	(*Aster dumosus*)

Tests of the soils supporting the above species in the pine-barrens have shown them to be practically throughout of the high specific acidity of 300.

The many writers on plant distribution who regard physical factors as dominant in determining the distribution of plants would find difficulty in explaining the occurrence of species normally found in fertile meadows or upon rock ledges, in the sterile shifting sands and damp depressions of this coastal area along with characteristic peat bog plants. It seemed worth while, therefore, to ascertain whether any light could be thrown on the matter by a study of the chemical features of the several soils concerned.

The soil of the salt-marshes is of course decidedly alkaline in reaction because of the calcium bicarbonate in the sea water; actual tests by the indicator method showed a specific alkalinity of about 30. Hummocks extending above the water level show less alkalinity, but rarely reach neutrality. At the contact of the marsh with the sands of the mainland or islands it might be expected that the reaction would change gradually from alkalinity to neutrality; for clean sand, made up of quartz and other practically insoluble minerals, of course is neutral. But such is not the case; the reaction changes sharply, within the space of a few centimeters, from a specific alkalinity of 30 to a specific acidity of 300; and the latter value is shown by the sandy soils of the bogs, plains, and dunes to distances of hundreds of meters back from the marsh margins.

The explanation of this change from alkalinity to acidity is not difficult to find, if approached, not from the frequent viewpoint that soil acidity is a high mysterious if not inscrutable phenomenon, but from a more modern one. As pointed out in the writer's paper above cited, when a solution of a neutral salt acts on a soil, both the clay and the humus present tend to adsorb the basic element from the salt, and to set free the acid. When the sea water is drawn up by capillarity, or distributed as spray by the wind to still greater distances from the shore, it yields to the soils some of its soda, and most of its lime and magnesia (compounds of bivalent elements being adsorbed more strongly than univalent ones), and as a result the soil acquires considerable acidity through the liberation of hydrochloric and sulfuric acids.[5]

It is accordingly possible to explain the occurrence in this coastal area of plants showing elsewhere widely divergent preferences as to habitat. The plants of list 1 evidently require in their soils an abundance of available lime and other bases, either free or in the form of salts, which requirement is here met; but they must be tolerant of high acidity. Those of the second list demand high acidity, which they find in the coastal area as well as in the pine-barrens; but they must be tolerant of the presence of salts. The other plants of neutral-soil upland regions, in so far as they have had an opportunity to migrate along the coast but have failed to do so, are presumably to be interpreted as intolerant of acidity, even though adequately supplied with lime; and other plants of the pine-barren area, which have had a chance to extend coastward, but have not become established within the range of abundant spray, are no doubt to be classed as unable to withstand the presence of salts, in spite of the existence of a suitable degree of acidity.

There is of course no reason why such phenomena should be limited to New Jersey; and Professor M. L. Fernald has recently called the writer's attention to the fact that plants found elsewhere in fairly acid soils occur at the edges of salt marshes in Massachusetts under circumstances which have not heretofore been fully understood. These relations were studied especially at the typical locality known as Oak Island, a few miles northeast of Boston.[6] This deposit of glacial debris in the midst of the salt marsh is occupied by a rich woods, with the typical upland flora shown in list 3 (list of species kindly furnished by Professor Fernald, common and American code names added by the writer).

LIST 3. PLANTS OF RICH WOODS, OAK ISLAND, MASSACHUSETTS

Slender wild rye	(*Elymus striatus*)[7]
Bottle-brush grass	(*Hystrix patula* (*Hystrix*))
Woolly sedge	(*Carex lanuginosa*)[7]
Canada lily	(*Lilium canadense*)
Trout lily	(*Erythronium americanum*)
Bellwort	(*Uvularia perfoliata*)
Showy orchid	(*Orchis* (*Galeorchis*) *spectabilis*)

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[5] The chemical substances are here referred to by the familiar terms lime, magnesia, hydrochloric acid, etc., although it is of course recognized that the phenomena observed are due directly to the *ions*; that is, lime is adsorbed as calcium-ion, a solution of hydrochloric acid reacts acid because of the free hydrogen-ion present, and so on.

[6] WM. P. RICH, "Oak Island and its Flora." Rhodora, 4: 87. 1902.

Blunt-leaf sandwort	(*Arenaria* (*Moehringia*) *lateriflora*)[7]
Strong-scented meadow rue	(*Thalictrum revolutum*)[7]
Red baneberry	(*Actaea rubra*)
Shrubby bittersweet	(*Celastrus scandens*)[7]
Honewort	(*Deringa canadensis*) (*Cryptotaenia canadensis*)
Sweet cicely	(*Osmorrhiza* (*Washingtonia*) *longistylis*)
Fringed loosestrife	(*Steironema ciliatum*)
Richweed	(*Collinsonia canadensis*)
Figwort	(*Scrophularia marilandica*)
Wood betony	(*Pedicularis canadensis*)
Lopseed	(*Phryma Leptostachya*)
Horse gentian	(*Triosteum aurantiacum*)
White rattlesnake root	(*Prenanthes* (*Nabalus*) *alba*)

The soil of this woods showed, when tested, a low degree of acidity, averaging a specific acidity of 3, the high content of lime and other bases in the glacial material from which the soil is derived evidently preventing the development of high acidity. The salt-marsh mud proved, as usual, to have a specific alkalinity ranging from 30 (wet portions) to as low as 3 (hummocks). Between the woods and the salt-marsh is a strip of damp ground a meter or two in width, supporting a flora quite unlike that of either woods or salt-marsh; instead, the species were found to be those elsewhere characteristic of peat bogs, sandy or peaty margins of ponds, sandy barrens, etc. A list of these (also by Professor Fernald, with common and American code names added by the writer) follows in list 4; not all of the species are known to grow on Oak Island, but such as do not are found in quite similar places on the Massachusetts coast.

LIST 4. PLANTS OF UPPER BORDER OF SALT-MARSH, AT OAK ISLAND AND OTHER POINTS ON MASSACHUSETTS COAST; USUALLY FOUND INLAND IN PEAT OR WET SAND, EXCEPT AS NOTED.

Bog club-moss	(*Lycopodium inundatum*)
Switch grass	(*Panicum virgatum*)[8] (in damp sand)
Blue-joint grass	(*Calamagrostis canadensis*) (also in swamps)
Green spike-rush (sedge)	(*Eleocharis olivacea*)[8] (also in wet bogs)
Three-square sedge	(*Scirpus americanus*)[8]
Twig-sedge	(*Cladium* (*Mariscus*) *mariscoides*)[8]
Canada rush	(*Juncus canadensis*)[8]
Turks-cap lily	(*Lilium superbum*)
Grass-pink orchid	(*Limodorum tuberosum*) (*Calopogon pulchellus*)[8]
Pink bearded orchid	(*Pogonia ophioglossioides*)[8]
Cross-leaf milkwort	(*Polygala cruciata*)[8]
Inkberry	(*Ilex glabra*)[8]
Sweet pepper-bush	(*Clethra alnifolia*)[8]
Privet andromeda	(*Xolisma ligustrina*) (*Lyonia ligustrina*) (also in dry barrens)

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[7] Found also in the coastal area of New Jersey.

Highbush blueberry	(*Vaccinium corymbosum*)[8] (also in dry barrens)
American cranberry	(*Vaccinium* (*Oxycoccus*) *macrocarpon*)[8]
Buckbean	(*Menyanthes trifoliata*) (also in wet bogs)
Large gerardia	(*Agalinis* (*Gerardia*) *purpurea*)[8]
Small gerardia	(*Agalinis* (*Gerardia*) *paupercula*) (also in dryish sands)
Small bedstraw	(*Galium trifidum*) (also in wet bogs)

What a fine chance this was, we thought, for anyone who wished to deny the influence of acidity on plant distribution to get evidence apparently favorable to his view. No one could doubt that the salt-marsh muck is moderately alkaline, and everyone would be willing to admit that the rich woods soil might be slightly acid. The intervening strip of damp ground would naturally be inferred to be approximately neutral in reaction. Now, the vegetation of this strip is, as above noted, elsewhere characteristic of damp sandy or peaty places where the soil is admittedly highly acid. Clearly then, one might reason, these plants grow in both habitats because they find there the proper physical conditions, the optimum moisture content of the soil, for their best growth. Are they not, therefore, supremely indifferent to the fact that the acidity is several hundred times as great in the one habitat as in the other?

The tests of the reactions of the soils with the indicators spoiled this line of reasoning, however, by destroying the premise from which it started. The reaction of the intermediate strip, lying, it will be recalled, between a slightly acid soil on the one side and a moderately alkaline one on the other, proved to be nowhere near neutral in reaction; it was found to be instead strongly acid, specific acidity 300, just like the average sandy barren and peat bog. The reason for the development of this acidity at the border of the salt-marsh is of course the same as for that found in the New Jersey localities: the sea water is drawn up by capillarity into the soil around the edge of the woods, its bases are adsorbed by the clay and by the humus, and acids are set free. If the plants of list 4 really require high soil acidity, then they can get it here as well as in any other of their habitats.

That the occurrence of the plants of list 4 in soils of acidity 300 is a matter of preference and not mere tolerance to high acidity is clearly indicated by the fact that the majority of these plants are not known to grow in any habitat of a much lower degree of acidity than this. In habitats such as stream banks and pond borders where the reaction is but weakly acid and no peat is forming, even though the water content of the soil is as near as may be to that in the places where they flourish; these plants are conspicuously absent. It can only be concluded from these relations that the majority of the plants in list 4 grow at the border of the salt-marsh and in wet sandy and peaty places because of the presence in both of these habitats of highly acid soils.

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[8] Found also in the coastal area of New Jersey.

[*Note.*—Does not the acidity of the soil, which herein is shown to so strongly influence plant distribution, also influence the distribution of the animals living in the soil? Here is a problem for cooperation between the botanist, zoologist and chemist.

Progress in plant ecology has been seriously hampered by the theory that the important, if not the only soil factors influencing plant distribution, are the physical properties of the soil. Dr. Wherry's interesting paper should go far toward destroying this fallacy and stimulating soil research along chemical lines. Another paper by the same author explaining the cause of soil acidity and giving a simple field method for determining it will appear in ECOLOGY.—EDITOR.]

THE ESTABLISHMENT OF A DOUGLAS FIR FOREST[1]

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Douglas fir (*Pseudotsuga taxifolia*) has gained and held possession of by far the greater part of the forested area of the Cascade and Coast region of Washington and Oregon. The dominant position of this tree in the plant formations of the region has not been attained through any one characteristic, but rather through ability to overcome many varying and extreme conditions through a grouping and regrouping of a number of characters. This varied combination of characteristics gives Douglas fir a wide range of adaptation and a resultant superiority over its associates.

The seed of Douglas fir is peculiarly sinted for regeneration, and in favorable seed years which occur at irregular periods, is produced in large quantities. When the seed crop is light the seeds are generally attacked by an insect (*Megastigmus spermotrophus* Wachtl) which destroys before maturity a large percent of the few seeds which would otherwise be produced. Heavy seed crops are advantageous, because the seeds of this species are the favorite food of rodents. This paradox is explained by the fact that, with a heavy crop, the surplus produced over the amount consumed by rodents is large, and is stored away by the rodents in the duff and mineral soil of the forest floor, in caches varying in size from a few seeds to bushels of cones. These caches are not used in the fall, and before the following spring all traces of the rodents' work have been eliminated by the snow and rain. The seeds are thus preserved in their natural storage of cool temperature and moisture conditions which reduce the oxygen content of the soil. How long the seed will remain viable in this natural storage is not known. Experimental evidence has proved it to be viable after six years, but it may lie an indefinitely longer period. These conditions demonstrate the biological relations of the forest which must not be overlooked in the study or control of either the flora or fauna of a region.

In the forest, seeds which remain near the surface and receive favorable germinating temperatures will germinate, but the seedlings do not become established. The Douglas fir is not a shade enduring species, especially in cool situations. Consequently, it has very little chance to reproduce under a forest canopy. This character eliminates it as an under story, and is the underlying factor which makes the Douglas fir a one-generation tree in the

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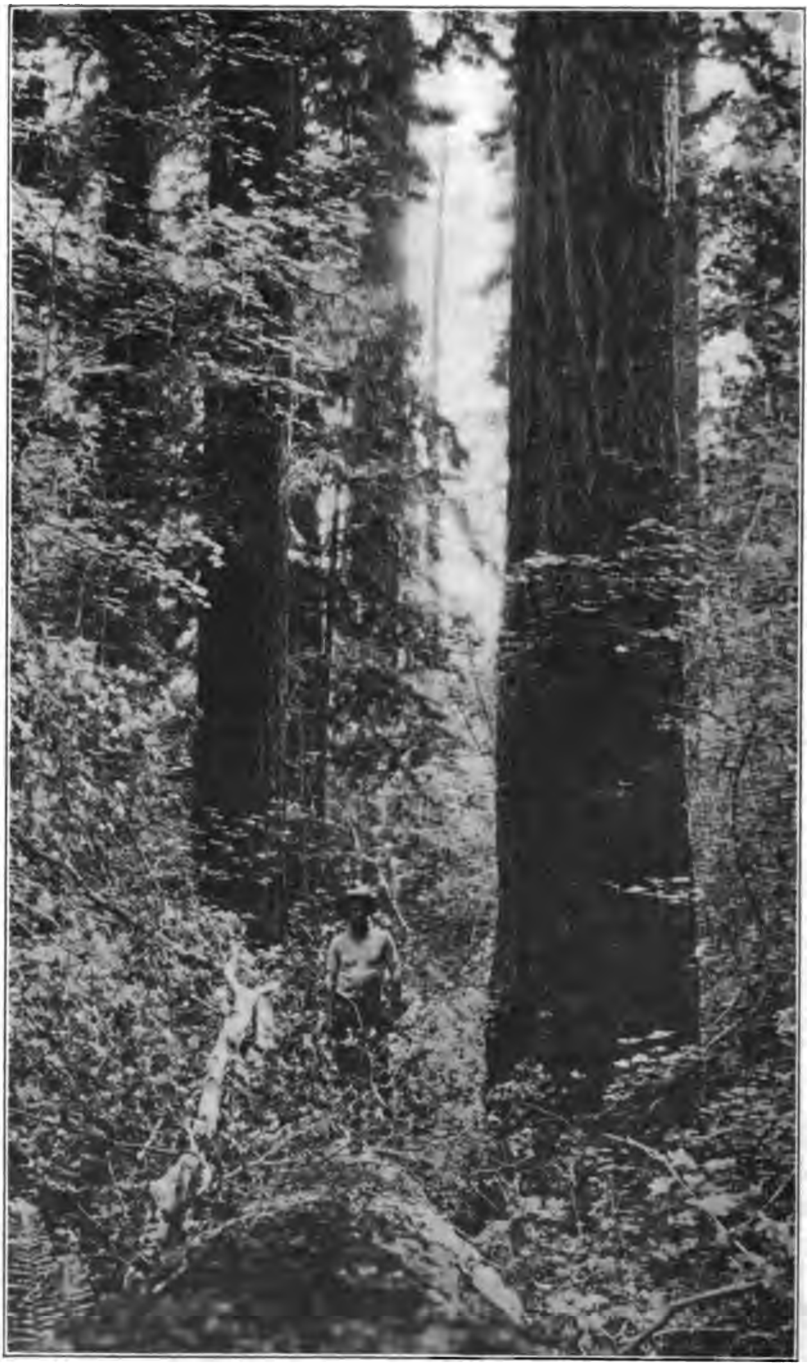
[1] Presented before the St. Louis meeting of the Ecological Society of America in December, 1919. Published by permission of the Secretary of Agriculture.



Photograph by Barrington Moore, 1913.

FIG. 1. A typical forest of Douglas fir (*Pseudotsuga taxifolia*) more than 200 years old but still thrifty. Picture taken from top of a log four feet in diameter owing to undergrowth of vine maple. Winberry Creek, Cascade National Forest, Oregon.

natural cycle of this formation. In the establishment of a sere the Douglas fir appears through only one generation, while its associates, the western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) may be represented by several generations during the stages of succession, and be reproduced indefinitely after the *Thuja-Tsuga-hylium,* which is the climax forest, is established. This condition is brought about by the shade-enduring characters of the cedar and hemlock during all stages of their development.

With such a large percent of the extensive cedar-hemlock climax forest occupied by a Douglas fir formation, the significance of factors other than competition is emphasized. The Douglas fir formation (*Pseudotsuga-hylium*) is not, as might appear, a retrogression from the cedar-hemlock climax, but is rather the stage of succession preceding the climax.

The principal combination of factors responsible for the preponderance of the Douglas fir formation is the presence of seed stored in the forest floor, and of fire. When the forest is removed by fire, or by cutting, the stored seed is left under favorable germination conditions and immediately responds to the stimuli. The result is an immediate replacement by the species which occupied the ground before the fire. The proportions of the species in the young growth may vary from the proportions of the previous mature forest. An important factor in this variation of proportion of species is the amount of seed cached by the rodents. Larger amounts of Douglas fir seed are cached than of hemlock or cedar, which gives this species an advantage after the forest is removed. The same holds true of the western white pine (*Pinus monticola*).

The seeds of the white pine are relished by rodents and are greedily gathered and stored. So pronounced is this influence that often Douglas fir and western white pine make up as much as 75 percent of the young growth where the mature stand contained only 2 percent of these species. The removal of a forest results in changed conditions of soil moisture and temperature and local changes in atmospheric conditions. These changes often produce a xerophytic site where a mesophytic site prevailed while the area was forested. The drying out of sites is also a favorable factor in assisting the Douglas fir to conquer its associated species. The Douglas fir seed germinates quickly under favorable conditions, and the seedling produces a long radicle during its early stages of growth. This is so pronounced compared with hemlock and cedar that it enables the Douglas fir to become established where the others fail.

On dry sites, such as the large Cispus burn of 1918, northwest of Mt. Adams, where nearly 150 square miles of forest were burned over, the ability of establishment often determines the species of the forest during the first stages of succession. The ability of the Douglas fir to develop a root system 6 to 8 inches deep during the early part of its first growing season is an important factor in retaining the Douglas fir formation.

This is proved by the soil moisture readings and the wilting coefficient of Douglas fir seedlings. On the south slope the surface soil moisture reached a minimum of .18 percent in July and did not go above .85 percent in August, while at a depth of 6 inches the south slope soil contained 6.55 percent moisture in July and 5.50 percent in August. The wilting coefficient of 2-year-old Douglas fir seedlings was found to be 1.25 percent for this soil.[2]

It is obvious from these data that seedlings could not germinate or live in the surface layer of soil, since the moisture content was below the requirement of the seedlings. At a depth of 6 inches, however, there was sufficient moisture for growth all through the season. Consequently, any seedlings with roots penetrating to the 6-inch depth would become established.

The soil is mostly a volcanic ash, very loose and porous, and is underlaid with rock or clay at depth of 2 to 6 feet on the slopes.

On the flat river valleys the soil contains a silt loam which lowers the wilting coefficient but does not retain sufficient moisture in the surface soil to secure germination or establishment. The surface soil contained .19 percent of moisture in July and .09 percent in August, and the wilting coefficient of Douglas fir 2-year-old seedlings was found to be .94 percent for this soil. At 6 inches the soil contained 11.45 percent of moisture in July and 9.32 percent in August. Obviously, then, seedlings must have root systems which penetrate to a six inch depth before July in order to become established in this region. These conditions of moisture confine the shallow-rooted seedlings of hemlock and cedar to the most favorable slopes and the moist draws.

The extreme soil moisture conditions are readily explained by the soil temperature and evaporation.[3] The soil on the south slope reached a maximum of 128° F. in July and 135° F. in August. The evaporation on the south slope from July 15 to October 1 was 1,070 cc. as compared with 690 cc. on the flat, that is, more than one and one half times as much on the flat. With such extreme temperature and moisture demands only those Douglas fir seedlings which are protected by shrubs or annuals survive the first one or two dry seasons and become established.

After a forest canopy is formed and duff accumulates on the surface, the site becomes more mesophytic, and cedar and hemlock are again able gradually to encroach on the Douglas fir forest. In this way the cedar and hemlock under story is established, permitting the Douglas fir to be the dominant tree only during the first generation except in the localities which cedar or hemlock do not reach by migration until two or more generations of Douglas fir have occupied the ground.

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[2] [It would be interesting to know if the wilting coefficient of Douglas fir differs from that of wheat. Briggs and Shantz evidence of the similarity of the wilting coefficient of different plants (U. S. Dept. Agr. Bu. of Plant Industry, Bul. 130, 1912) has never, so far as we know, been experimentally disproven.—EDITOR.]

[3] Evaporation records were taken with the Bates' Type 4 Evaporimeter.

SUMMARY

The measurable characteristics of the Douglas fir, which give it such a prominent place in a formation of which cedar and hemlock comprise the climax forest, may be briefly stated: The production of heavy crops of seed which is the favorite food of the indigenous rodents; caching of seed by rodents in the forest floor; ability of the seed to retain its viability while stored in the forest floor and to live through forest fires; early and quick germination of the seed under favorable conditions; and a rapid development of a long radical.

The unfavorable factors are the inability of the Douglas fir to withstand shade, which results in its elimination from the under story of the forest and consequent elimination from the climax forest.

These factors are within the control of man, and it is on them that the scientific management of Douglas fir must be based in order to keep the Pacific Northwest region under continuous natural production of this most important species.

[*Note.*—Are the rodents protected in Washington and Oregon, or are they being exterminated? The proper handling of rodents becomes of great importance in reproducing the Douglas fir, and is a subject for cooperation between foresters and zoologists. Reproduction of western yellow pine (*Pinus ponderosa*) from seed stored by rodents has been noticed by the editor on the east slope of the Cascade Mountains in Oregon. What other forests show reproduction by the same agency? EDITOR.]

NOTES AND COMMENTS

The address of the Secretary of the Society will be "Puget Sound Biological Station, Friday Harbor, Washington" from June 20 to August 15.

COMMITTEE OF THE SOUTHWEST

Last summer preliminary steps were taken by the Ecological Society towards a cooperative study of natural openings or "parks" in the western yellow pine (*Pinus ponderosa*) forests of Arizona and New Mexico. These "parks" are of considerable importance in the forest management of the region. Their cause remains unknown in spite of the attention which has been given them. It has become evident that the problem can be satisfactorily solved only by cooperation, and the Society is therefore endeavoring to bring together those interested in the work. The United States Forest Service and the Carnegie Institution of Washington have agreed to cooperate, thereby making it possible to apply the promising method of soil areation investigations developed by Cannon and Free.

The Fort Valley Forest Experiment Station which is conducted by the Forest Service at Flagstaff, Arizona, is on the edge of a typical park in the yellow pine forest. Here a conference of all those interested in the problem will be held in May or June. All members of the Society who are interested and wish to cooperate, may secure the necessary information from Professor Weese, Secretary of the Society (University of New Mexico, Albuquerque), who is cooperating as zoologist, or from Dr. Forrest Shreve in Tucson, who initiated the project last summer. The following statement by Dr. Pearson in charge of the Fort Valley Experiment Station, who is representing the Forest Service, outlines briefly the work done on the problem prior to the present cooperation:

"This subject has received more or less attention at the Fort Valley Experiment Station in connection with various forest problems, but as yet no serious effort has been made to arrive at an explanation for the existence of parks. All of the studies have been made in the large park near the Experiment Station. This park, which is really a valley or basin, is typical of one class of treeless areas within the yellow pine forest. There is a local distinction between "parks" and "prairies." Prairies are, as a rule, larger in extent and usually they are not lower than the surrounding timbered areas as in the case of parks. The study should cover both types of open areas.

From 1909 to 1913 inclusive, meteorological records, including temperature, precipitation, wind movement, relative humidity and evaporation, were maintained at two stations in the park and one in the forest near the experiment station. Soil moisture and soil temperature records were kept during a portion of the above period. The results were published in 1914.[1] Among the conclusions are the following:

Minimum temperatures are commonly from 10 to 15° F. lower in the park than in the forest.

Wind movement and evaporation are much higher in the park.

The soil freezes to a greater depth in the park.

The snow melts more gradually in the forest.

The above factors are known to have an important bearing upon the absence of trees in the park. Determinations of soil moisture and wilting coefficient (centrifugal method) yielded no definite conclusions. Recent studies, however, indicate that the soil factors are important.

Attempts at artificial reforestation with 3-year-old transplants have been partially successful. The plants make a vigorous growth during the summer, but usually the tops are killed back in winter. Winter killing is thought to be closely related to the deep freezing of the soil. Another factor is the presence of a hard pan which prevents deep root penetration. Hard pan, however, does not occur everywhere in this park, nor is it characteristic of all parks and prairies.

During the past ten years a considerable number of natural pine seedlings have come into evidence in certain portions of the Fort Valley park. Some of these are two or three feet tall, but few are more than three years old. The taller plants exhibit a tendency toward winter killing similar to that observed in planted stock. This form of injury is less common in small seedlings probably because they remain covered with snow during the period when the soil is frozen.

What data have been secured indicate that the conditions most responsible for the failure of seedlings to establish themselves in parks are to be found in the soil. Physical texture as determined by the presence or absence of sand, gravel and stones, appears to be very important. Undoubtedly permeability to water and air is a vital factor. Chemical analyses have thus far furnished no clue, but this subject should receive further attention. Root systems should be examined with special reference to depth of penetration under different conditions."

Pacific Coast Meeting

The Pacific Division of the American Association for the Advancement of Science will hold its fourth annual meeting at Seattle on June 17–19, in quarters to be provided by the University of Washington. The program contemplates a session of three full days, with the affiliated societies' meeting in the forenoons and the general sessions in the afternoons.

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[1] Pearson, G. A., "A Meteorological Study of Parks and Timbered Areas in the Western Yellow Pine Forests of Arizona and New Mexico." Monthly Weather Review 41: 1615–1629, 1914.

Arrangements are being made for participation on the part of the Ecological Society in a symposium on the Fisheries of the North Pacific Coast, with the Western Society of Naturalists and the Pacific Fisheries Society. This symposium will be held Thursday afternoon, June 17. It is planned, also, to hold a joint session with the Western Society of Naturalists for the reading of papers of general ecological interest, and, if the number of titles submitted is sufficient, an additional meeting of the Ecological Society will be held. Excursions to points of interest will probably be arranged for Saturday, June 19. It is hoped that the attendance of members residing in the western states and of others who are able to be present will be large, and that the meeting may be a successful one.

Members who wish to present papers should send titles to the Secretary as soon as possible. Titles should, if possible, be accompanied by a brief abstract of the paper, and a statement as to time required and facilities needed for the illustration of the paper.

Preservation of Natural Areas

The Ecological Society has been offered an unusual opportunity to serve biological science. The Executive Committee of the Division of Biology and Agriculture of the National Research Council has had under consideration the matter of reserving natural areas for biological study, and has voted to refer it to the Ecological Society. The Committee on the Preservation of Natural Areas for Ecological Study, and Committee on Cooperation of the Society considered the problem and presented a report to the National Research Council.

National Research Council

The following letter indicates the attitude of the National Research Council toward scientific societies Any suggestions for matters to be brought before the Council will be welcomed.

National Research Council,
Washington, D. C.,
March 22, 1920

Dear Doctor Moore:

According to word recently received from Doctor Weese, Secretary of the Ecological Society of America, there has been appointed a committee on cooperation to work with the Division of Biology and Agriculture of the National Research Council. I wish to express my pleasure and satisfaction in this action of your Society and also the hope that through our combined efforts we may accomplish much good for the subject of ecology in this country. Several of the societies have for some time had such relations with our Division and already the experience has been helpful and promises to develop into one of our best means for promoting our efforts. The fact that the National Research Council is constituted through the medium of our national societies makes our progress dependent upon the strength and activity of these organizations. It is to the interest of our sciences, therefore, that we bring to the solution of our problems the combined and coordinated efforts of all available agencies.

We shall accordingly hope to have from your committee any suggestions that recommend themselves and will desire to refer to you for advice such matters concerning ecology and related sciences as require expert attention. We would particularly wish your consideration of the larger and more fundamental questions which demand solution before we can make satisfactory progress in meeting the enlarged responsibilities and opportunities which the war has left us. Will you be kind enough to bring these matters to the attention of the other members of your committee and see that they are informed regarding the organization and activities of the National Research Council? We have sent them general information about the Council but they should be fully informed in relation to the particular aspects which concern ecology.

With the earnest hope that we may reasonably meet these tests upon our fitness through cooperative action, I am

Sincerely yours,
C. E. McClung, *Chairman,*
Division of Biology and Agriculture.

Scientists in Government Service

The Congressional Joint Commission on Reclassification of Salaries, created over a year ago, submitted its report, a large volume of more than 1000 pages, to Congress on March 12, 1920.

The report furnishes conclusive evidence that employment conditions in the Federal Government are at present more or less chaotic. Compensation for the same character of employment varies widely, and Government workers in general are much underpaid as compared with those in similar work elsewhere. These conditions have resulted in a steadily increasing flood of resignations, particularly in the scientific-technical force, which has seriously impaired the efficiency and threatened the integrity of the entire service.

The rate of separations, or personnel turnover, in the Government service in Washington has increased from 5.5 percent in 1904, to 11.4 percent in 1916, and to 50 percent in 1919, the most conspicuous advances being among the scientific and technical employees. In the Bureau of Standards the rate of increase in the turnover among the scientific employees jumped from 28 percent in 1916 to 161 percent in 1919, and it is becoming more and more difficult to fill vacancies on account of the apathy of scientific and technical men toward the Government service.

The Commission has provided a classification of positions in the Government service in the District of Columbia whereby all employees engaged in approximately the same character of work and carrying approximately the same degree of responsibility will receive substantially the same salary, the salaries recommended being what it regards as "equitable." Provision is made for the administration of the classification by the Civil Service Commission, as the central personnel agency for the Government, and for the first time an attempt is made to inaugurate a comprehensive and uniform employment policy.

In the classification of professional employees in the scientific-technical group, the statements of duties and qualifications have been so framed as to bring about a real coordination between those with similar training and experience but engaged in different lines of work. Five main classes have been recognized, which are designated:

Junior Plant Ecologist (or Forester, or Chemist, or Bacteriologist, or whatever the particular line of work may be)
Assistant Plant Ecologist
Associate Plant Ecologist
Plant Ecologist
Senior Plant Ecologist

Since the chief differences between these classes lies in the amount of responsibility, either administrative or substantive, involved, a statement of the duties and qualifications of a single class will indicate the general character of them all. Thus, the specifications for the class known as Assistant Plant Ecologist read as follows:

Duties.—To perform, under supervision, scientific work in plant ecology, and related work as required.

Examples: Making accurate measurements of physical factors influencing plant succession; conducting experiments in reforestation; determining the conditions under which, by natural means, the prevailing plant types in a given environment may be advantageously modified; studying the mutual interaction of plant formation and physical environment; searching scientific literature; taking notes and writing progress reports.

Qualifications.—Training equivalent to that represented by graduation with a degree from an institution of recognized standing, with major work in botany and ecology; at least two years' graduate work, or, in the absence of graduate work, practical experience regarded as its full equivalent; ability to read scientific German, and, in addition, French, Swedish or Russian.

The salaries are as follows for the different classes:

Junior	$1,800–$2,160	per year
Assistant	2,400– 3,000	" "
Associate	3,240– 3,840	" "
Full professional	4,140– 5,040	" "

No salaries were recommended for men in the senior class or for chiefs of bureau, these salaries being left for determination by Congress on the recommendation of the Civil Service Commission and the head of the Department concerned. Taking the scientific-technical group as a whole, the average salaries recommended represent an increase of about $1,000 per year for each individual in the group, or of more than 40 percent over the present average. This is the largest percentage increase recommended for any group of employees outside of the teachers in the public schools of the District of Columbia.

This fact, as well as other points brought out in the Commission's report, indicate that it recognized the importance of the scientific-technical group in the Government service. Thus the letter of submittal emphasizes the fact that the employees in the highest administrative, scientific, and professional classes "are the real leaders of the civil service of the Republic." The desirability of adopting a liberal policy in the personal restrictions placed on these employees, and of encouraging scientific work, is shown in the following paragraph:

"Finally, every effort should be made to stimulate initiative and originality on the part of scientific and other professional workers. It is peculiarly appropriate that the Federal Government should take the lead in research work of all kinds; but it can not do so unless it is able to attract and retain independent thinkers of the highest type. The reduction of red tape to the minimum, the encouragement of freedom of thought and action to the maximum, and the direction of research by thoroughly trained investigators would all assist to make this possible."

PROCEEDINGS

The Ecological Society held its annual meeting with the American Association for the Advancement of Science at St. Louis, December 30, 1919, to January 1, 1920, inclusive. The program was as follows:

COMMITTEE ON COOPERATION: [BARRINGTON MOORE, Chairman; C. C. ADAMS, and T. L. HANKINSON, New York State College of Forestry; G. P. BURNS, Vermont Agricultural Experiment Station; and NORMAN TAYLOR, Brooklyn Botanic Garden] Plants and Animals of Mt. Marcy, New York.

Studies of the alpine vegetation reveal that of 67 species of flowering plants found above the timber line only about 23 are true alpines, the balance of the vegetation being composed of plants from lower elevations, which, changed in stature, color and ability to set seed, are gradually encroaching over the mountain-top. Forty years ago only 53 species were recorded from the summit. Fourteen additional ones have been recently discovered, nearly all of which are apparently migrants from below timber line.

STEPHEN E. WILLIAMS, Miami University. Observations on the habits of larval colonies of *Pectinatella*. (A. S. Z.)

V. E. SHELFORD, Illinois Natural History Survey. Hydrogen ion concentration in the different stages of pond succession. 15 min. (E. S. A.)

The discussion will cover the plants and animals present; H ions in different stages; the reactions of fishes to H ions in relation to succession; comparison of ponds with streams and bayous; seasonal differences.

W. C. ALLEE, Lake Forest University. Animal Aggregations. (A. S. Z.)

A. D. HOWARD, U. S. Bureau of Fisheries. Distribution of life on a river bottom. 15 min. (E. S. A.)

In an investigation to determine the distribution of fresh-water mussels a somewhat detailed study was made of the whole bottom in a portion of a river. The area studied was a three-mile section of one channel of the Mississippi River between Rock Island, Illinois, and Muscatine, Iowa. The river in this section is comparatively straight and of rather uniform character (gradient, depth, etc.) passing over soil of clay, sand and sendimentary rock (mostly limestone).

The life on the bottom was found to have a rather definite distribution with reference to physiographic features of the river. In general this benthos was restricted to a zone 200 feet wide along each shore. Where islands occurred a narrower zone was found along the shores of the islands. This zone apparently had no particular relation to depth of water as the middle area of the stream, about 500 feet wide, was no deeper than the 200 feet strips along shore. The latter are by no means equally productive throughout. The more densely populated portions are unquestionably distributed in relation to definite positions of the channel and other features; the channel being defined as the main body of flowing water in the river following usually the more excavated portion of the stream bed. On account of the changeableness of the channel in sandy sections of the river, features which insured permanency of condition were found an important factor in the bottom life at any given place.

The productive areas were usually parts of the shore strips that were bathed by the current; that is, in general, where the channel approaches the shore. Character of soil was a determining feature as in other bodies of water but this is often controlled by current, relation to channel, topography, and such features. The possibility of greater food content of the water at the more productive areas was considered but not investigated in this particular locality as there seemed to be no reason for expecting it to be an important variable here. Doubtless, there is some local affect. from contributions of the banks and the plankton of small tributaries.

In the life zones variation from swift to comparatively slow water were observed accommodating species adapted to these varied habitats.

Chauncey Juday, Wisconsin Natural History Survey. Behavior of the larvae of *Corethra punctipennis* Say. (A. S. Z.).

A. D. Howard, U. S. Bureau of Fisheries. Changes observed in river fauna above Keokuk Dam. 15 min. (E. S. (A.)

Keokuk Lake five years after its formation by the dam across the Mississippi River was examined to determine some of the effects of the changed conditions. In the portions of the lake occupying the bed of the river it was possible to examine productive life areas and compare the conditions with those existing in the former river. Some lands flooded by the elevation of the water have since been reclaimed by dyking. These give the opportunity to study advantageously the extension of pioneer aquatic species in the brief interval of submergence. Animals in the productive life areas of the former river-bed are subjected to a considerable decrease in current, an increase in depth of water with a heavy precipitation of fine black mud. Collections very obviously show the suppression of characteristic river species and the increase of pond or lake dwelling forms. A conspicuous increase in aquatic plants as compared with the usual river flora was observed.

Leslie B. Arey, Northwestern University, and W. J. Crozier, University of Chicago. On the natural history of *Onchidium.* (A. S. Z.)

Royal N. Chapman, University of Minnesota. Ecological succession of insects in stored food products. 15 min. (E. S. A.)

A. A. Schaeffer, University of Tennessee. On a new principle underlying movement in organisms. (A. S. Z.)

H. C. Cowles, University of Chicago. The rising rock shores of northern Lake Michigan. 20 min., lantern.

Lake Michigan has many examples both of building shores and eroding shores. The chief building type is the sandy shore with its associated dunes, perhaps unequalled in their display of vegetation types. The chief eroding type is represented by the cliffs of glacial clay. Especially northward there are building shores of sand mixed with wood drift, of shingle, and of silt. Eroding rock shores are relatively infrequent and are best displayed in Door County, Wisconsin, which forms a peninsula between Green Bay and Lake Michigan. The shores of northern Lake Michigan are noted for their considerable elevation during post glacial time. That rapid elevation is still continuing has been appreciated only recently, and the best measure of the rate of rise is furnished by the plants that invade the bared surfaces. The region also furnishes a good instance of a progressive succession rapidly accelerated by a favorable physiographic change. A sinking shore, as in parts of Lake Erie, illustrates retrogressive succession.

J. V. Hofmann, U. S. Forest Service. The establishment of a Douglas Fir Forest (*Pseudotsuga taxifolia*). 15 min.

The Douglas fir has gained and held possession of the greater part of the forested area of the Cascade and Coast region of Washington and Oregon. Its dominant position has been attained not through any one characteristic but by its ability to overcome many varying and extreme conditions through a grouping and regrouping of a number of characters, giving the tree a wide range of adaptation. The seed of Douglas fir is peculiarly adapted for regeneration. Those remaining near the surface and receiving favorable temperatures will germinate, but the seedlings do not become established. The tree is intolerant of shade, especially in cool situations. When the forest is removed by fire or cutting the stored seed is left under favorable conditions for germination. The ability of Douglas fir to develop a root system 6 to 8 inches deep during the early part of its first growing season is an important factor in its establishment.

C. C. Adams, New York State College of Forestry. The Roosevelt Wild Life Forest Experiment Station,—a new ecological station. 20 min.

W. A. Cannon, Desert Labortory. Some characteristics of precipitation in arid regions. 10 min.

One of the characteristics of the storms of northern South Australia is the relatively large proportion of the annual rainfall which occurs in separate storms too small to benefit plants. Thus at Oodnadatta, where the annual precipitation is 4.68 inches, so much as 56.7 percent of this may occur in storms each of which would amount to .15 inch or less. Such rains do not penetrate the ground sufficiently, neither does the soil remain wetted long enough, to be made use of by the roots either of annuals or of perennials.

C. A. SHULL, University of Kentucky. Changes in the vegetation of Kentucky. 10 min. (B. S. A.)

W. A. CANNON, Desert Laboratory, and E. E. FREE. Soil aeration and growth of roots. 20 min., lantern. (E. S. A.)

Experimental work on the root reaction of species to soil atmospheres of different compositions indicate that the roots of land plants of various habits and from a variety of habitats, may exhibit reactions which are different but wholly consistent and characteristic. At one end of the series stands *Coleus,* and possibly *Covillea,* which are extremely sensitive to oxygen deprivation and to large amounts of carbon di-oxide, and at the other end *Salix* and *Eucalyptus,* which are indifferent, either to the one or the other. Among the gases used were nitrogen and helium and it was found that those employed contained a small amount of oxygen, nitrogen about .5 percent, and helium about .2 percent. The latter gas effected root growth less injuriously than the former. This difference in behavior is ascribable to the more rapid movement of oxygen in helium than in nitrogen. The rate of oxygen supply therefore is of greater importance than the oxygen pressure *per se.*

FRANK C. CATES and ALICE E. KEENER, Kansas State Agricultural College. Red coloring in the leaves of *Diervilla lonicera.* 7 min. (B. S. A.)

GEORGE D. FULLER, University of Chicago. An edaphic limit to forests in the prairie region of Illinois. 15 min., lantern. (E. S. A.)

A soil survey has shown the existence of two soil types in the prairie region of Illinois. One type has as its vegetation grassland, the other forest. The soil of the forest is similar to the subsoil of the prairie areas but is better drained. Its extent is related to the amount of stream erosion and so strictly is the forest limited to this type as to lead to the conclusion that here at least the character of the soil is the factor in deciding the limits of tree growth.

ARTHUR G. VESTAL, Eastern Illinois State Normal School. The vegetation component as the unit in mixed associations. 12 min. (B. S. A.)

EDITH B. SHREVE, Desert Laboratory. Seasonal changes in the water relations of desert plants. 15 min. (E. S. A.)

The daily march of transpiration and of leaf-water content were measured for a perennial (*Encelia farinosa*), a winter annual (*Streptanthus arizonicus*) and a summer annual (*Amaranthus palmeri*) for the seasons in which they live. *Streptanthus* is living in January and February under the most arid conditions it can endure and has no means of coping with the much more arid conditions of June. *Encelia* is able by some internal regulation to keep its loss of water per unit area down to only 1.4 times as much in June as in January, although the ratio of evaporation to soil moisture is 4.5 times as great in the former month. *Amaranthus* can withstand a greater aridity than *Streptanthus* but can not endure the arid conditions of September, which are only one-third as severe as in June.

FRANCIS RAMALEY, University of Colorado. Some mountain plant communities of sandy soil. 15 min. (B. S. A.)

J. E. WEAVER, University of Nebraska. Correlation between the root development of cereals and grassland associations. 20 min. (E. S. A.)

Studies of the root development of winter wheat (*Triticum aestivum*), oats (*Avena sativa*), and winter rye (*Secale cereale*) have been made at 13 stations in the states of Colorado, Kansas, Nebraska, and South Dakota. These stations are all in the prairie-plains grassland formation and were selected as typically representative of conditions in the three grassland associations. One group in eastern Nebraska lies in the true prairies (*Stipa-Koeleria* association) which is dominated by tall sod-forming grasses and is further characterized by an abundance of herbaceous societies. Another group in Colorado and western Kansas represents short-grass plains vegetation (*Bulbilis-Bouteloua* association) where tall grasses are practically absent and relatively few, poorly developed, herbaceous societies are found. The third group in central Kansas and western South Dakota is located in the mixed prairies (*Stipa-Bouteloua* association) where tall and short grasses meet on somewhat equal terms, the latter forming an understory to the taller grassy and herbaceous vegetation.

The results of examination of the average stem height and the working depth and maximum depth of roots in 44 fields reveal the fact that there is a direct correlation between cereal crop plant development and the environment as expressed in the development of the natural vegetation. In true prairies crop plants reached their greatest stem and root development; in the short-grass plains the least; while growth in the mixed prairies was intermediate.

W. B. MCDOUGALL, University of Illinois. Perennial root-hairs of *Gleditsia* and related genera. 5 min. (B. S. A,)

C. A. SHULL, University of Kentucky. The formation of a new island in the Mississippi River. 7 min. (E. S. A.)

During the last six years an island has been forming in No. 5 shoot of the Mississippi River, the channel which separate Wolf Island from the Missouri bank of the river, almost opposite Columbus, Ky. The island is now somewhat over a half mile in length, and about an eighth of a mile in average width. Its area is in the neighborhood of fifty acres, and it stands high enough to require a 43-foot stage of the river to inundate it. It is covered with a very fine growth of young cottonwoods, about three inches in diameter and twenty-five feet tall. The history of the island is remarkable, as it is known to have been started by a barge which stranded on a rock bar in No. 5 shoot during the recession of the great flood of 1913. This barge formed the original obstruction to the current which caused deposition, and is now completely buried near the head of the island.

FRANK D. KERN, Pennsylvania State College. Some recent observations on the dissemination of the barberry. 6 min. (B. S. A.)

A. E. Douglass, University of Arizona. Evidence of climatic effects in the annual rings of trees. 12 min., lantern. (E. S. A.)

The rings of the yellow pine in northern Arizona show varying thickness in marked correlation with rainfall; the sequoias of California show similar characteristics in less degree. Climatic effects may also be detected by similarity in ring-growth over large areas. A characteristic called "mean sensitivity" is suggested as a possible measure of climatic reaction.

T. J. Fitzpatrick. The fern flora of Nebraska. 10 min. (B. S. A.)

Norma E. Pfeiffer. Ecological relations of the genus *Isoetes*. 15 min. (B. S. A.)

Bruce Fink. The taxonomic and biologic relations of the Graphidaceae. 15 min. (B. S. A.)

Adele Lewis Grant. A discussion of the genus *Mimulus*. 15 min. (B. S. A.)

Edwin B. Payson. Geographical distribution of the genus *Lesquerella*. 10 min. (B. S. A.)

The business meeting of the Ecological Society of America, held in the Soldan High School, St. Louis, Missouri, was called to order at 2:30 P.M. on December 31, 1919, by the President, Major Barrington Moore.

The address of the president was then delivered.

The report of the retiring secretary-treasurer, Forrest Shreve, was read by the acting secretary. This report is printed below.

Upon motion duly seconded the report was accepted.

In response to a request from Prof. F. R. Lillie, chairman of the Committee on Cooperation in the Division of Biology and Agriculture of the National Research Council, it was moved, seconded, and resolved that the present committee on cooperation of the Ecological Society consisting of Major Moore, chairman, and Messrs. C. C. Adams, Geo. P. Burns, T. L. Hankinson, Norman Taylor and H. L. Shantz be instructed to act as an advisory committee in cooperation with the Division of Biology and Agriculture of the National Research Council.

The committee on the preservation of natural conditions for ecological study reported through its chairman V. E. Shelford that progress was being made and requested that the committee be continued and authorized to make the necessary expenditure for preparing its report.

It was moved, seconded and resolved that the report of progress be accepted and the committee continued. No written report was submitted.

The question of whether the Society undertake, at the present time, the publication of a journal was brought before the meeting by the President and a discussion followed which was participated in by Messrs. MacDougal, Burns, Adams, Livingston, Cowles, Waterman and others.

It was moved and seconded that the annual dues of the society be for the future $2.50.

It was moved in amendment that the amount of the annual dues be $3.00. The amendment was seconded and carried.

It was moved, seconded and resolved that the offer of the Plant World Association to turn over that journal to the Ecological Society be accepted and that the Plant World be made the official organ of this society.

It was moved, seconded and resolved that the subscription price of the Plant World be in the future $3.00 but that the present subscribers be permitted to renew their subscription for 1920 at the present rate of $2.50.

It was moved, seconded and resolved that a second class of non-subscribing members be created and such members be accepted for a period of not more than three years each at an annual fee of $1.00 each. Such members shall be expected to become subscribing members at or before the expiration of three years and are only then entitled to receive the journal of the Society.

It was moved, seconded and resolved that the president of the society be directed to associate with himself two others to act as a committee to confer with a committee from the Plant World Association upon all matters relative to the taking over of the Plant World, and that this committee be given full power to act in all matters relating to the editing and publishing of this journal as the official organ of the Ecological Society.

The chairman of the committee on nomination of officers, Prof. H. C. Cowles, submitted the following recommendation for officers for the ensuing year:

President: Major Barrington Moore,
Vice-President: George E. Nichols,
Secretary-Treasurer: A. O. Weese.

Moved, seconded and carried that the acting secretary be instructed to cast a ballot for the list of officers recommended by the committee on nominations. The ballot was cast and the officers declared duly elected.

Upon motion duly seconded, it was resolved that the secretary be instructed to convey to the retiring secretary, Forrest Shreve, the high appreciation of the Ecological Society of America for his faithful and most efficient service during these early and critical years of its existence.

The President announced as the additional members of the committee for taking over the Plant World Messrs. C. C. Adams and Norman Taylor.

The meeting then adjourned.

GEORGE D. FULLER,
Acting Secretary

REPORT OF SECRETARY-TREASURER FOR 1919

Meetings.—The last regular meeting of the society was held at Baltimore in Convocation Week 1918, and a summer meeting was held on June 19 and 20 at the Throop College of Technology at Pasadena, California. At the former meeting joint sessions were held with the American Society of Zoologists and the Botanical Society of America, and at the latter meeting with the Western Society of Naturalists and the Cooper Ornithological Club.

Field Trips.—During the past year no field trips have been held under the auspices of the Society. More extended work was done in the field, however, by five members of the Committee on Cooperation, at Mt. Marcy, New York. It is to be hoped that the return of normal conditions in our educational institutions will enable us to resume field excursions in different parts of the country. The holding of such excursions was one of the primary objects in the formation of the Ecological Society, and their value needs no demonstration.

Bulletin.—The bulletin was changed in 1919 from monthly to bi-monthly appearance, and six numbers have been issued.

Membership.—Twenty-three new members have joined the Society in 1919 and two resignations have been received, making the present membership 370.

Arrears of Dues.—It is found that the number of members in arrears for 1917 is 35, for 1918 is 63, and for 1919 is 110. It is suggested that no action be taken at present regarding the members who are two years in arrears, as letters have recently been written which will call the attention of the delinquents to this matter and will doubtless be the means of saving them to the membership of the society.

Committees.—The standing investigative committees of the society are as follows:

Committee on Cooperation: Barrington Moore, Chairman.

Committee on the Preservation of Natural Conditions for Ecological Study: V. E. Shelford, Chairman.

Committee on Soil Temperature: Forrest Shreve, Chairman.

The resignation of Dr. A. S. Pearse as chairman of the Committee on Fresh Water Fish and Fisheries has resulted in no further action by that committee.

Finances.—The income and expenditures of the society during the past year have been as follows:

Income:		
Balance from 1918	$ 31.73	
Dues and subscription to Bulletin	292.50	
Refund on stationery	3.80	$328.03

Expenses:

Assistant Secretary	$ 75.00	
Committee on Preservation	19.53	
Committee on Soil Temperature	4.50	
Affiliation Fee, Pacific Div. A. A. A. S.	5.00	
Printing Bulletin	80.75	
Miscellaneous printing	12.00	
Stationery	9.65	
Postage	22.63	
Express, telegrams and incidentals	20.35	249.41
Balance on hand		$ 78.62

The above statement does not include cost of printing the program of the St. Louis Meeting, for which bill has not yet been rendered. The dues now in arrears afford a potential asset of $208.

Respectfully submitted,
FORREST SHREVE,
Sec'y-Treasurer

TUCSON,
December 26, 1919

REPORT OF COMMITTEE ON SOIL TEMPERATURE

FORREST SHREVE, *Chairman;* ALFRED E. CAMERON

This committee has now been engaged for three years in an effort to obtain, through cooperative observers, as large a series of soil temperature data as possible. The original plans for the work of the committee called for a series of well distributed stations throughout the United States and Canada at which soil thermographs should be run at stated depths and under conditions as nearly comparable as possible with respect to soil texture, character of surface, slope exposure and drainage. Very loyal and enthusiastic cooperation has been secured from persons both in and outside the Ecological Society, and any value that may attach to the assembled results stands much more to the credit of the cooperators than to that of the committee.

The list of 29 stations published in the Bulletin for February, 1918, indicates the original scope of the observations. Unfortunately seven of these stations have been discontinued, chiefly through the movement of the observers to other fields of work, and partly through the policy of the Forest Service to abandon some of their investigative laboratories, which had unfortunately been placed in the midst of National Forests in close proximity to the problems which they were designed to investigate. At four of the stations it has not been possible for the cooperators to continue their observations throughout the year. At five others it was impossible to secure thermographs, and readings with soil thermometers have been made.

The original plan of the soil temperature survey called for readings at a depth of 3 inches or else at 12 inches, or at both depths. At two stations we have fine series at these two depths. Most of the thermograph data are for 3 inches, while most of the thermometer readings are for 12 inches. The stations at which more than one thermograph is in operation are those at Burlington, Vt., maintained by Prof. George P. Burns, and at College Park, Md., under Dr. A. G. McCall; while at Flagstaff, Ariz., Mr. G. A. Pearson is maintaining valuable series of thermometer observations at several depths as well as at several altitudes on the San Francisco Peaks. Prof. C. W. Edgerton, at Baton Rouge, La., has also obtained two series on different types of soil.

Owing to the fact that many of the cooperators have an interest in the data secured, in connection with their own work, it has not been possible to hold all of them to the depths at which it was desired to secure the observations. This results in the possession of several fine series of thermograph records which are not comparable with those of any other stations. While such data are of some value in themselves they do not contribute to the information necessary for the construction of a map of the soil isotherms of the United States and Canada, which it was hoped at the outset would be one of the final concrete expressions of the cooperative work of the committee.

It was originally planned to carry on the work of the committee for only three years. As it is still desirable to secure fresh stations and especially continued readings at the proper depths, and as all of the cooperators are taking such enthusiastic interest in the work, it is the hope of the committee that the Society will feel moved to authorize a continuation of this cooperative investigation. Two new stations have recently been secured in the United States and three in Canada, the records from which will add very materially to the value of the survey because of the critical points at which the stations are located.

The cost of the work of this committee for the past year has been $4.50. The records of the observers have been inspected and tabulated, and it seems desirable to publish at an early date some of the figures which are now in hand.

The committee will greatly appreciate information regarding any readings of soil temperature that have been taken in the past, and will welcome the cooperation of any members of the society.

Respectfully submitted,

FORREST SHREVE,
Chairman

TUCSON, ARIZ.,
December 26, 1919

ANNOUNCEMENT

The arrangement by which The Plant World is continued under the name *Ecology,* as the official publication of the Ecological Society of America, will not affect the previously existing arrangements for supplying back numbers and sets of the former journal, and the separates and other publications which have recently been offered. It is not possible to supply the first seven volumes. Volumes 10 and 11 can be supplied only in incomplete condition. All other volumes are $2.50 each. Single numbers are 30 cents each. All separates and publications can be supplied at previously advertised prices. A price-list of publications will be sent on application. All paper should be made payable to The Plant World and all orders should be addressed to

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The Ecological Society of America

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AIMS

The Ecological Society of America was founded in 1915 for the purpose of giving unity to the study of organisms in relation to environment, as a means of furthering intercourse between persons who are approaching widely different groups of organisms from closely related points of view, for the stimulation of ecological research, and to assist the development of the utilities which may be served by ecological principles.

MEMBERSHIP, DUES, AND PRIVILEGES

Membership is open to those who are interested in the advancement of ecology or its applications, and to those who are engaged in any aspect of the study of organisms in relation to environment.

Dues are $3.00 per annum. Members are entitled to receive Ecology, to present papers at meetings, to vote at meetings and in letter or other balloting, and are eligible as officers and as members of committees.

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ECOLOGY

CONTINUING THE PLANT WORLD

OFFICIAL PUBLICATION OF THE

ECOLOGICAL SOCIETY OF AMERICA

VOLUME I, No. 2 APRIL, 1920

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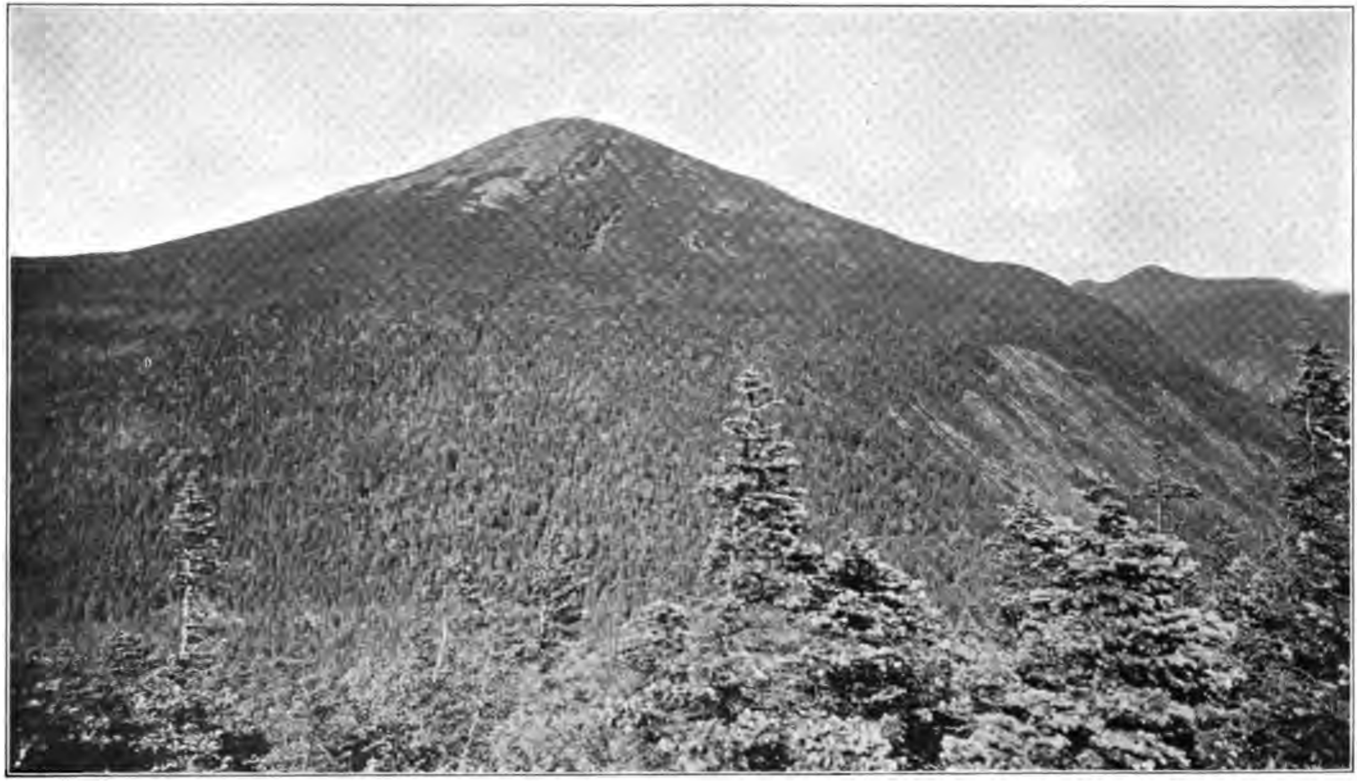

Frontispiece

By courtesy of the New York State Conservation Commission

Mount Marcy looking north from Mt. Skylight.

ECOLOGY

VOL. I APRIL, 1920 No. 2

PLANTS AND ANIMALS OF MOUNT MARCY, NEW YORK, PART I

CHARLES C. ADAMS, GEORGE P. BURNS, T. L. HANKINSON, BARRINGTON MOORE, AND NORMAN TAYLOR[1]

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I. THE PROBLEM

The purpose of the present investigation was to bring to bear upon the problem of timber line on mountains the methods of study and knowledge of botanists, zoologists, and foresters in order to learn more of the relation of plants and animals to their environment. Timber line gives a comparatively sharp line of demarkation between different habitats, which can here be readily contrasted; also the factors of the environment causing this differentiation of habitats can be studied to advantage along the line where their influence is so marked.[2] The severity of the conditions to which organisms are subjected above timber line gives a splendid opportunity for studying the effects produced by the environment upon the plants and animals which have been able to withstand these conditions.[3] Furthermore it is necessary to consider organisms in relation to their past history, and the zone above timber line is a promising place for investigations on post-glacial migration.[4] Hence timber line on Mt. Marcy in the Adirondack Mountains of New York was chosen as a favorable locality for this cooperative study. The elevation of Mt. Marcy is 5,344 feet, the highest of any point in New York State.

---

[1] Members of the Committee on Cooperation of the Ecological Society of America, chairman Barrington Moore. The institutions cooperating and authors representing them were: the Brooklyn Botanic Garden (Taylor), Roosevelt Wild Life Forest Experiment Station of the New York State College of Forestry at Syracuse (Adams and Hankinson), Vermont Agricultural Experiment Station (Burns). Valuable assistance in the field arrangements, with the Ausable Club as a base, was rendered by Mr. Alfred T. White, chairman of the Governing Committee of the Brooklyn Botanic Garden.

Observation and correlation were largely used in this investigation; instrumental records over a brief period were also secured for air temperature, soil temperature, evaporation, and solar radiation. These records, though insufficient for absolute comparisons, yet have a distinct relative value in showing differences between critical points in the vegetative covering of the mountain.

DEFINITION OF TIMBER LINE USED IN THIS STUDY.—There is no *absolute tree line* on Mount Marcy, since stunted trees grow in patches practically up to the summit. But there is what may be called a *timber line,* that is a line at which the forest cover stops, giving place to open vegetation with clumps of stunted trees in the depressions. *For the purpose of this study the timber line is considered as the beginning of alpine vegetation except in ravines and other depressions. Characteristic alpine plants of Mt. Marcy are Empetrum nigrum, Rhododendron lapponicum, Diapensia lapponica, Solidago Cutleri, and Vaccinium caespitsum.* The timber line as above defined occurs at between 4,800 and 4,900 feet, mostly near 4,900 feet, and, where not interfered with by ravines and slides, extends around the mountain with remarkable regularity. There is no sharp distinction between north-facing and south-facing slopes as in the mountains of the West, the absence of this contrast in the Adirondacks probably being due to the abundant rainfall which masks the differences in insolation.[5] Ravines extend up the mountain carrying the forest in a continuous body above the timber line. These ravines are sometimes so wide as to create the impression that solid timber extends above 4,900 feet. Yet even here a difference seems to occur at an elevation of between 4,800 and 4,900 feet, for at about 4,890 feet the trees become considerably shorter and more stunted. Looking from above at one of these ravines, the change in the character of the trees at timber line can be clearly seen.

---

[2] Much has been written on the environment above timber line. For a brief discussion see C. H. Shaw's "Vegetation and altitude," Plant World, Vol. 12, No. 3, pp. 63–64, 1909, and "Causes of timber line on Mountains," Plant World, Vol. 12, No. 8, pp. 169–181, 1909.

[3] See paper on "Anatomical reduction in some Alpine plants," by C. C. Forsaith, in this issue for an interesting piece of work on this subject.

[4] Adams, Charles C. "Postglacial origin and migrations of life of Northeastern United States," Jour. Geography, Vol. 1, No. 7, pp. 303–310, 1902.

————. "The postglacial dispersal of North American Biota," Biol. Bull., Vol. 9, pp. 53–71, 1905.

————. "Migration as a factor in evolution: its ecological dynamics," Am. Nat., Vol. 52, Oct.–Nov., 1918, and 53, Jan.–Feb., 1919.

Scharff, R. F. "Distribution and origin of life in America," MacMillan, New York, 1912.

II. The Region

Mount Marcy.—Mount Marcy lies in the eastern Adirondacks about 25 miles west of Lake Champlain. The mountain in profile is a low cone, with the upper few hundred feet forming a low dome. A general view of the south slope of the mountain, from Mount Skylight, is shown in the frontispiece, and a view of the upper part of the north slope, mainly above timber line, is shown in figure 1. The eastern and southeastern sides are more precipitous.

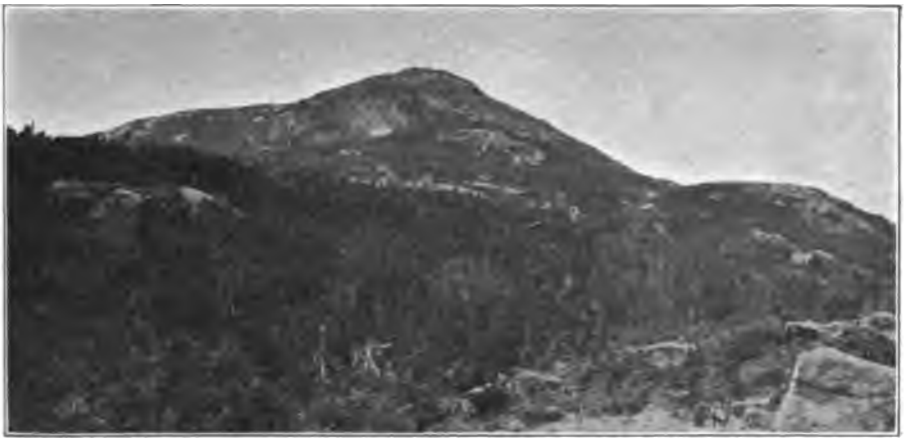
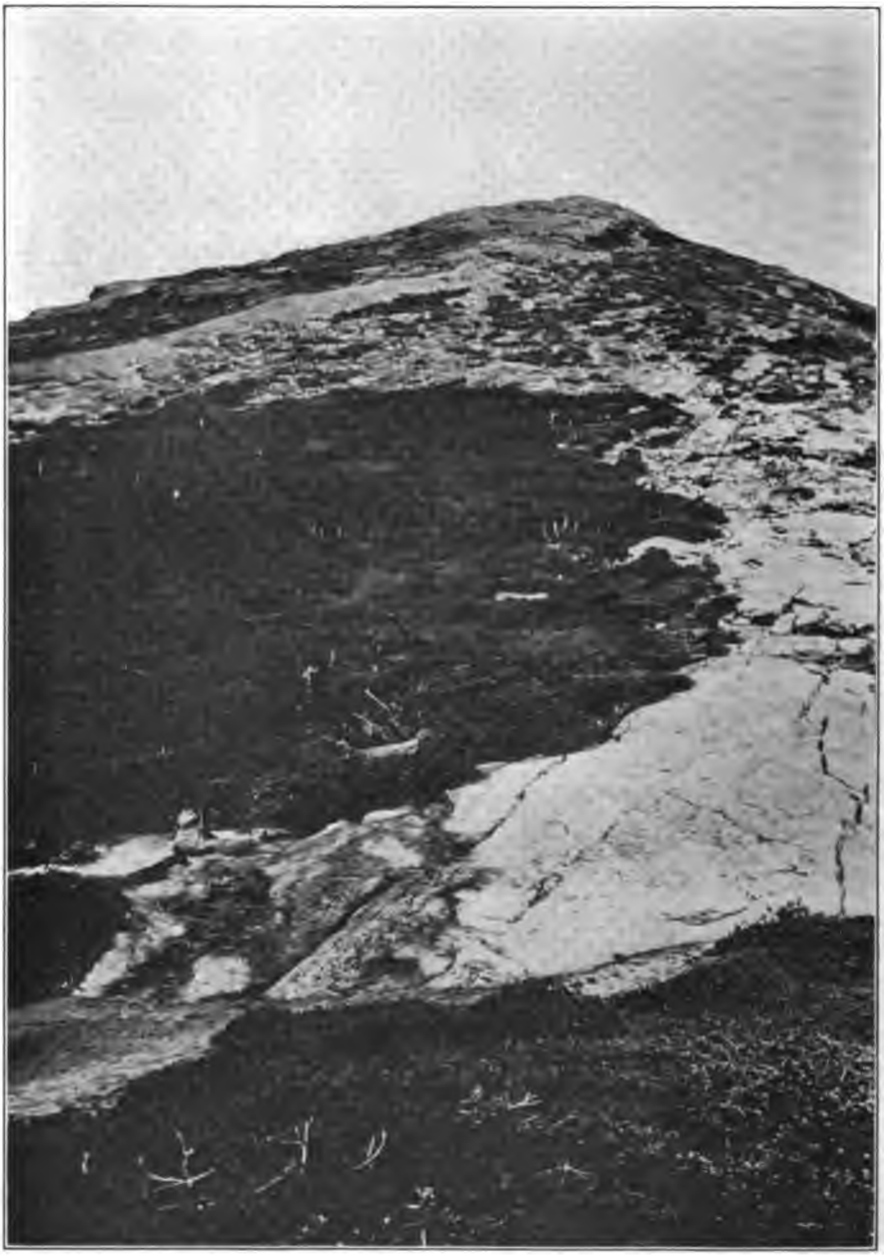


Fig. 1. North slope of Mt. Marcy from 4,850 feet elevation. Just below the summit on the left is the cirque containing a snowdrift; photographed June 5, 1919.

The conspicuous topographic features of the mountain above timber line are, ecologically considered, its isolation, its relatively small area and its relatively uniform relief. The isolation gives exposure on all sides. The domed surface favors rapid drainage, and the elevation into the cloud zone favors precipitation. There is a sphagnum bog on the northeast slope at about 5,000 feet, and a well-defined cirque (fig. 1) on the same slope at an elevation of 5,250 feet, later described and illustrated as the "Dwarf birch meadow." On the southwestern slope is a large ravine, which reaches to near the top of the mountain. The southeastern and eastern slopes are more

---

[5] Measurements of the rate of drying of the forest floor on north and south slopes are given by S. B. Show in his "Climate and forest fires in northern California," Journal of Forestry, Vol. 17, No. 8, pp. 965–979, 1919. Even greater contrasts are found in the Southern Sierras and in Arizona and New Mexico.



By courtesy of the New York State Conservation Commission.

FIG. 2. Southern trail slope of Mt. Marcy above timber line from 5,000 feet elevation. Stunted balsam fir in a depression in the foreground.

precipitous. The southern trail slope (fig. 2) contains much loose, bare rock and has the appearance of active snow slides. The vegetation below, to the southeast, supports this inference by the injury shown on the stunted balsams. The upper slopes are more stabilized, and when not bare rock or cut by rock and ice slides, are usually clothed with low vegetation, such as shown in figure 3. The cirque is in the lee of the mountain top and is located where snow would be expected to accumulate on account of the prevailing winter winds. This basin has diversified the alpine habitat by making conditions favorable for one of the alpine meadows, while joints or faults are apparently the cause of the formation of the meadows on the southeastern slopes. The rounded dome of the remainder of the mountain-top gives enough stability to the substratum to allow a few alpine meadows to develop.

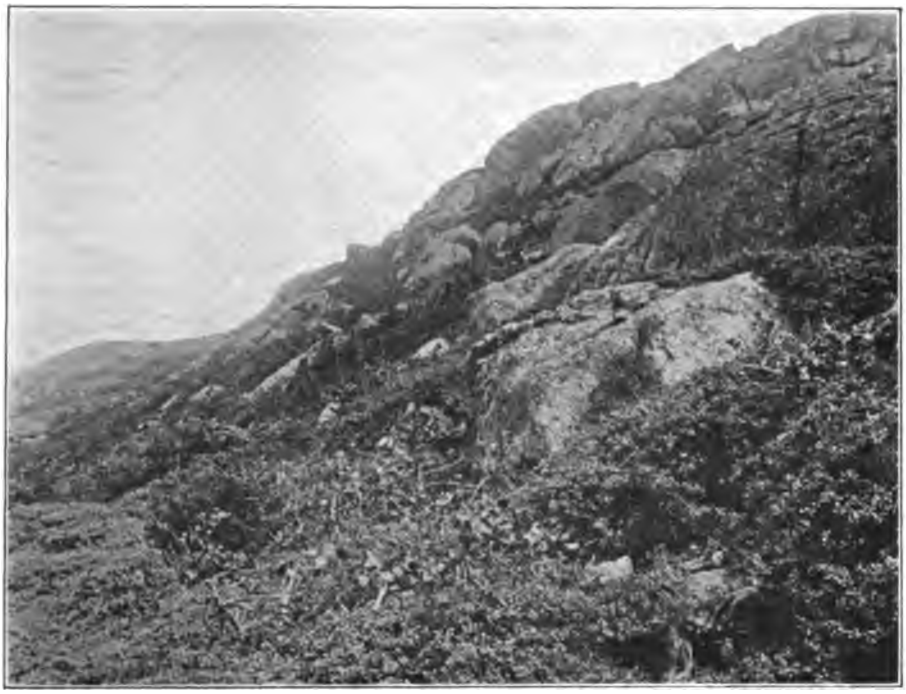


FIG. 3. Upper slopes of Mt. Marcy, showing alpine vegetation with stunted balsam firs in the sheltered spots.

TOPOGRAPHIC AND GEOLOGIC RELATIONS.—The culminating mountain peaks of eastern North America are Mount Mitchell, in the Southern Appalachians, with an elevation of 6,711 feet, Mount Washington, of the White Mountains (6,279 feet), and Mount Marcy or Tahawas (Indian for "Cloud-Splitter") of the Adirondacks, with an altitude of 5,344 feet. The topographic features of the Adirondacks may be summarized as follows:

The Adirondack region is a plateau formed by the uplifting of a peneplain, which now stands at an elevation of about 2,000 feet. Upon this dissected, tilted and much fractured upland arise, in the eastern part, the highest mountains of the Adirondacks. These were probably, in part, monadnocks upon this peneplain before it was elevated. The primary relief of the region is due to the partial development, from this plateau by erosion, of a later lower peneplain, in the main below 2,000 feet, combined with tilting and extensive faulting of mountain blocks, and to cutting and filling by glacial ice and waters. The postglacial changes are relatively slight, including a depression of the region, a re-elevation, the cutting of stream gorges, and the filling of depressions by inwash and organic debris.

The geological history of Mount Marcy, as a part of the Adirondacks, is wonderfully interesting, and certain phases are ecologically significant today. The region is one of the oldest mountain forming areas in the world, and the present mountains are only the latest ones. In fact, they may be considered the truncated stumps or deep seated roots of the former mountains, whose thousands of feet of overlying rock have been elevated and eroded away, so that now the basal roots are exposed at the surface. Even in Precambrian time mountains were here formed and worn down; this was repeated in the Cambrian, and in the Ordovician (Taconic), and again with the Appalachian revolution. Most of these last formed mountains were reduced during the formation of the Cretaceous peneplain, but resistant remnants or monadnocks were preserved (as Marcy), which were later again strongly uplifted (Tertiary) and now form, in the main, the present plateau at 2,000 feet and the higher mountains. The remnants of the Cretaceous peneplain now stand at an elevation of about 2,000 feet, and the Tertiary peneplain, developed below that level. Faulting took place on a large scale, previous to the ice age, and explains many of the southeastward and northwestward facing cliffs. During the ice age there was a depression of the region, overriding by the ice, with scouring and filling by glacial ice and waters, and last of all a slight elevation, with increased erosion.

It may seem strange that down through the ages influences have been at work, many of which, even today, control the life of the plants and animals now living upon the mountain. Thus the ancient igneous rock (anorthosite), has by its resistance retarded erosion and, combined with uplifts, has preserved the elevation, while softer rocks have been removed. This elevation has conditioned the alpine climate, with its many factors. The composition of this rock also, with its varied elements, and its large per cent (10.8) of lime[6] is important. The hardness of this rock is such that the minerals are made available slowly, and the high percentage of lime fails to exert the influence which would be expected. The soils now forming on the mountain from rock fragments are intermingled with the black, acid, organic material and are therefore acid.

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[6] Kemp and Reudemann. "Geology of the Elizabethtown and Port Henry Quadrangles," Bull. N. Y. State Museum, No. 138, p. 32, 1910.

Kemp[7] has called attention to the fact that, through faulting, the higher Adirondacks have a northeast and southwest trend, supplemented by minor faults at right angles to these, which break up the ranges into individual mountains, and thus form saddles or gaps which influence animals. As he expresses it (p. 201), "The little cross-passes almost always have a well-defined bear or deer trail following through." Furthermore, the drainage is affected by such topography and has a direct influence upon aquatic life. We thus see that these physical characteristics, even though of remote origin, exert today a very direct control upon existing organisms. The duration of this mountain has not only maintained Alpine biotic conditions since the ice age, but has perpetuated also a plant and animal population, which are relics of the long ago.

GENERAL ASPECTS OF PLANTS.—The Adirondack region is densely forested, the lower elevations being now characterized by deciduous hardwood forests of beech, birch and maple, with an intermixture of red spruce, balsam fir, hemlock, arbor-vitae, white pine, and few scattered deciduous species. In general, trees of all ages are represented throughout the forest, although under virgin conditions the older trees take up the larger proportion of the space. Young growth is ample in all openings, and even under the shade, owing to the shade enduring character of most of the trees (virtually all but yellow birch). Such woods occupy large areas in the Adirondacks and the Catskills. Their composition and description lie outside the scope of this paper, except where they are replaced by other types of vegetation as one goes up the mountain. The forest floor is often very beautifully covered by myriads of ferns and wild flowers such as *Cornus canadensis, Clintonia borealis, Coptis trifolia, Linnaea Americana, Oxalis Acetosella, Solidago flexicaulis* and others (fig. 4). The typical shrubs are *Viburnum alnifolium, Viburnum cassinoides, Rubus odoratus,* with, of course other species less common.

As one ascends the mountain the hardwoods gradually thin out as to size and frequency of occurrence, being replaced by the red spruce, *Picea rubens,* and balsam fir, *Abies balsamea.* From about 4,250 feet up, which may be considered the upper limit of the red spruce, the balsam fir forms pure stands except for scattering paper birch, *Betula papyrifera.*

In his "Plants of North Elba,"[8] Peck has tabulated the species and families of flowering plants and ferns as follows:

---

[7] Kemp, J. F. "The physiography of the Adirondacks," Pop. Sci. Mo., Vol. 68, pp. 195–210, 1906. See also on the geology and topography of the Adirondacks, Miller, W. J., "The geological history of New York," Bull. N. Y. State Museum, No. 168, pp. 1–130, 1914; "The Adirondack Mountains," Bull. No. 193, pp. 1–97, 1917.

[8] Peck, C. H. "Plants of North Elba," pp. 1–266, Bull. N. Y. State Museum, Vol. 6, Number 28, June, 1899.

Families	71
Species	492

Modern segregation of species and the recent discovery of new kinds would probably bring the number somewhat higher, but the fact remains that the Adirondack region, judging by the only reasonably complete flora of it yet published, is characterized by a comparatively small number of species, the bulk of which are very common. Peck's flora included Mt. McIntyre, next to Marcy in altitude, but not Mt. Marcy.

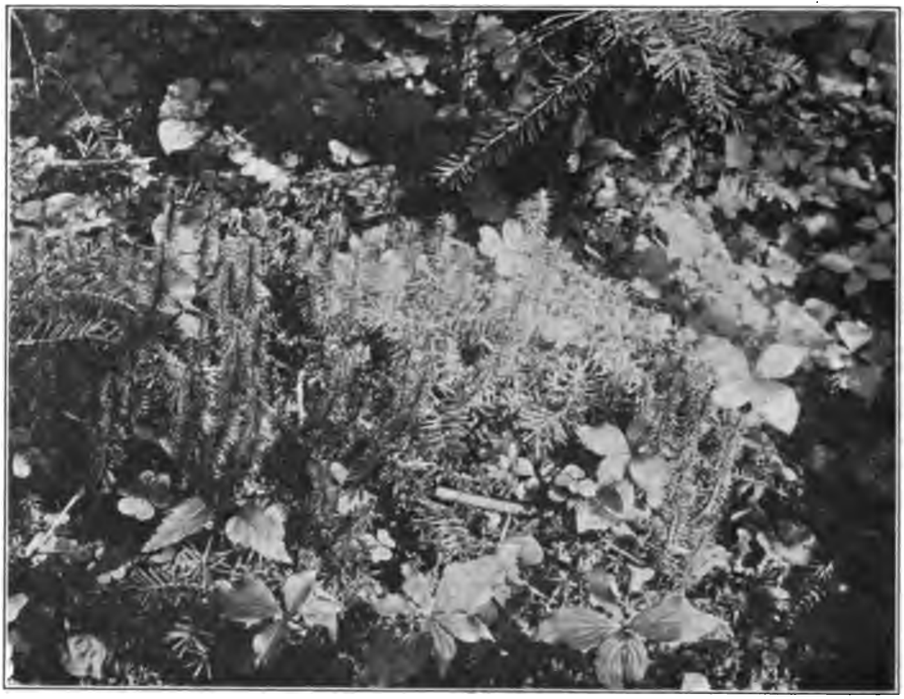

FIG. 4. Vegetation in small opening of pure fir forest at about 4,500 feet elevation, showing *Cornus canadensis, Oxalis Acetosella, Lycopodium,* and fir seedlings.

He included all introduced plants, and we have deducted these from his list, which then shows that 416 species constitute, without recent additions not yet tabulated, the actual wild flora of the mountainous part of the Adirondacks. The great bulk of these plants are of northern affinities, so that the general floristic composition of the region is fairly well indicated by the statement that the Adirondack flora is mostly northern with a limited number of species.

GENERAL ASPECTS OF ANIMALS.—In discussing the animals, in contrast with plants, allowance must be made for the fact that plants remain in evidence during stormy weather while animals tend, in general, not to be so active and attain their maximum activity during bright warm days, and then mainly during the warmest part of these days. The season (August) was also somewhat late for some species. Instrumental work and photographs further limited time for collecting. The relative scarcity of all kinds of animals was among the main features observed. This applied to both the invertebrates and the vertebrates. The scarcity of birds and mammals was conspicuous about our camp in the saddle at 4,355 feet, and these conditions seemed to hold up to the timber line. At camp there was a clearing due to the prolonged use of the site for that purpose. At Lake Tear a collection was made to get representative animals of an *open space,* and for comparison with the open mountain area above the timber line.

Above timber line the poverty of the fauna was very striking, and especially in the small number of animals that can be considered alipne. This is particularly noteworthy in connection with the animals mentioned by Colvin[9] (pp. 363–374) some of which have apparently since disappeared, as also have a number of plants mentioned by Peck as discussed below. The disappearance of the animals is, however, less certain than that of the plants because Colvin's notes were made largely in winter when there would naturally be more alpine animals which had come south. In general the collections suggested that the animals taken were an overflow from the richer lower level. We must look upon the peak of Marcy, with its relatively small area in a sea of forest, as a mere island of open. As a habitat the total area in the Adirondacks above timber line would equal only a small Adirondack lake. This open area in a forest region is somewhat (although inverted) similar to an open swamp or forest glade, and for this reason it is rather natural to expect in such conditions those animals which frequent the forest glades on warm days. The seasonal migration of animals up the mountain, as the season advances, favors just such concentration in the upper open places.

CLIMATE.—Colvin states that, if snow be the criterion, the summit of Mount Marcy enjoys barely two months of summer. Snow often whitens the mountain at the beginning of July, and a temporary covering comes in the first part of September. The climatic winter of the summit commences in the latter part of September or first of October, and ends in June.

No weather station records have been kept on Mt. Marcy and in trying to get some idea of the weather to which the mountain is subjected, the records from the stations nearest to it have been studied. These stations, with their airline distances from the summit of Marcy, and the elevation of them are as follows:

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[9] Colvin, V. "Seventh annual report of the topographical survey of the Adirondack region of New York, to the year 1879." Albany, 1880.

Gabriels	13 miles N.W.	1,729 feet
Lake Placid	7 miles N.	1,864 feet
Keene Valley	4½ miles N.E.	1,012 feet
North Creek	35 miles S.S.W.	1,002 feet
Indian Lake	37 miles S.W.	1,660 feet

Records from stations below 1,000 feet have not been used. A comparison of the records from these five stations, which have been kept over a period of years, shows a good deal of difference in the climate on the north and south-facing slopes of Marcy. Averaging the annual mean temperature shows 42.13° F. for the stations south of the mountain, and 39.54° for those north of it.

The minimum temperature for the stations north of the mountain, averaged over a period of years, is —36°, for the stations south of the mountain —28.4°., The snowfall for stations north of Marcy averages 127 inches (unmelted), while for those to the south it averages 78 inches a year. The maximum temperatures are much more uniform, averaging for the northern stations 92°, and for the southern ones 95°. No continuous records have been kept at the summit of Marcy, but Colvin mentions that a recording thermometer left there by him over the winter of 1875 registered —23°, but it was probably snow covered and "shows the minimum winter temperature of the rock at the summit rather than that of the air."[10]

Due to the precipitous topography, and the purely local nature of early and late frosts, the length of the growing season does not show such well-marked differences as temperature and snowfall appear to do between the north and south sides of the mountain. Taking the region of which Marcy is roughly the center, the growing season has averaged 92 days, compared with about 120 days in the Catskills, and over 200 on Long Island. The longest period has been 142 days; the shortest, 52 days. So far as the weather bureau records show, the latest frost in the spring came on July 20, the earliest on August 18, not, of course, in the same year.

These records give only a very general idea of the climatology of the Marcy region. The amount of variation from day to day, the differences between the south-facing and north-facing slopes, and the apparent waywardness of precipitation in its distribution is baffling if any general statement of the climate of the mountain is attempted. The precipitation is distributed rather uniformly over the year. Eight months have, at different times, shown the highest precipitation of the year. All months have shown the minimum at one time or another. On the whole the precipitation is high and sporadic.

The prevailing winds over a long series of years have been northeast or west, except that at Keene Valley they seem to be about evenly distributed between northwest and south.

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[10] Colvin, V. Loc. cit., page 328.

None of the figures cited give any real picture of the climate within the area of this study. The elevation is so much greater, the wind so much stronger, and the exposure near and above timber line relatively so great compared to the weather stations which are in the valleys. On June 5, 1919, near the summit of Marcy we found considerable unmelted snow. The general impression which even a brief period spent there gives, is that during the summer the precipitation is so plentiful that the forest floor just below timber line is wet a considerable part of the time. No one knows definitely how much of the time the mountain is cloud-capped; but certainly the humidity is greater than any records taken 3,500 feet below the summit would suggest. It is nevertheless possible that intervening dry periods may make moisture a limiting factor particularly in exposed situations above timber line.

III. Instrumental Data on the Local Environment

Stations and Instruments.—Certain of the factors that are known to influence the occurrence of plants and animals[11] are capable of measurement and study from the instrumental viewpoint, but the very position of the instruments on Mt. Marcy is naturally dictated by what the vegetation at different elevations shows to be critical points in the vegetative covering of the mountain.

These critical points, at least on the south side, are:

a. Lower limit of fir forest at 4,250 ft.
b. Bog at east end of Lake Tear, at 4,320 ft.
c. 1. Dwarf fir forest just below timber line, at 4,890 ft. in tree crowns.
  2. Same as 1 but on the ground under the forest to show conditions affecting reproduction.
d. Alpine zone above timber line, 4,900 ft. to summit, station at 4,920 ft.

Stations *a* and *b* are about a mile apart and about a thousand feet below the summit. Stations *c* (1 and 2) and *d* are only 75 feet apart and with a difference of but 30 ft. in altitude.

These different types of vegetation, quite unmistakable in their definiteness, and obviously the result of various factors, each occupy large areas on the upper slopes of the mountain, except the bog at Lake Tear which is probably not over 10 acres in extent.

The number and type of instruments used was limited by the practical problem of transportation from the base to the camp near the top of the mountain. For this reason it was impossible to use recording instruments. Evaporation and solar radiation were studied with the Livingston black and white spherical atmometer bulbs. It was not practical to use the rain correcting type. Accordingly, some of the bulbs were mounted on glass tubing which extended into a wide-mouth reservoir through a glass stopper. In this stopper was a second tube of somewhat wider bore which was flush with the bottom of the stopper and extended above the stopper about 1½ inches. This was the filling tube. On it a file mark was made and the distilled water in the reservoir was brought to a level with this mark. A 50 cc. burette was used in refilling the reservoir, and, owing to the small bore of the filling tube, very accurate readings were possible. To prevent water loss through the filling tube a cork stopper with a small groove along one side was used. The other bulbs had only one tube from the bulb to the reservoir and the file mark was made in the neck of the bottle. This type is less satisfactory, because it does not permit such accurate readings.

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[11] Our knowledge of the factors of the environment, and of how they act and how organisms respond, is still very inadequate, but is being increased with gratifying rapidity. Witness Garner and Allard's notable discovery of the control exerted by the relative length of day and night upon the growth and flowering of plants. (Garner, W. W., and Allard, H. A.. "Effect of relative length of day and night and other factors of the environment on growth and reproduction in plants." Jour. Agr. Res., Vol. 28, pp. 553–605, March, 1920.)

The water loss from the black atmometer was taken as an indication of the solar radiation because it is more influenced by light intensity than the other, and takes into consideration this additional factor, thus giving a more complete record of the complex combination of physical factors which make up a habitat.[12] The solar radiation was determined by subtracting the water loss of the white atmometer from that of the black, expressing the difference in cubic centimeters. Air temperatures were taken with the Weather Bureau type of maximum and minimum thermometers shaded from the sun. The soil temperatures were taken with a soil thermometer.

Station a.—This station was on a steep rocky mountain side facing northeast, at the lower limit of the fir forest where there is still an occasional large spruce representing the upper altitudinal limit of this tree. The reproduction was nearly pure fir (a more complete description of this forest will be found under IV, Plants and Animals). Below this station the spruce increases in proportion, while a short distance higher up it drops out completely. The atmometers were attached to the cut-off tops of fir saplings at a height of 8 to 9 feet above the ground in order to represent the crown conditions of young trees in openings of the forest. The surrounding trees were much higher, ranging up to 45 feet; but owing to the slope of the ground the instruments were fully exposed on the side away from the mountain except for about one hour each day. The topography allowed the sun to strike this slope for about two thirds to three quarters of the period it was above the horizon at this time of year. The thermometers were placed on a tree at 6 feet above the ground under a suitable shelter of boards.

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[12] The importance of solar radiation in controlling transpiration is shown in Briggs and Shantz "Hourly transpiration rate on clear days as determined by cyclic environmental factors." Jour. Agr. Res., Vol. 5, 584–649, 1916, in which they state (p. 647) that "radiation may be looked upon as the primary causative factor in the cyclic changes."

Station b. Lake Tear bog in which this station was located occupies an open area which is nothing more than a widened part of the depression between Mt. Marcy and Mt. Skylight, sheltered on all sides by the surrounding forest and on the northwest and southeast by the mountain slopes as well (See fig. 5). The vegetation consists of bog plants, several alpines, and a few isolated fir trees. The atmometers were placed in the open with their reservoirs buried in the dense mat of sphagnum, the bulbs about 5 inches above the surface of the moss. The thermometers were fastened to an adjacent fir tree at about the same level as that of the atmometer bulbs.

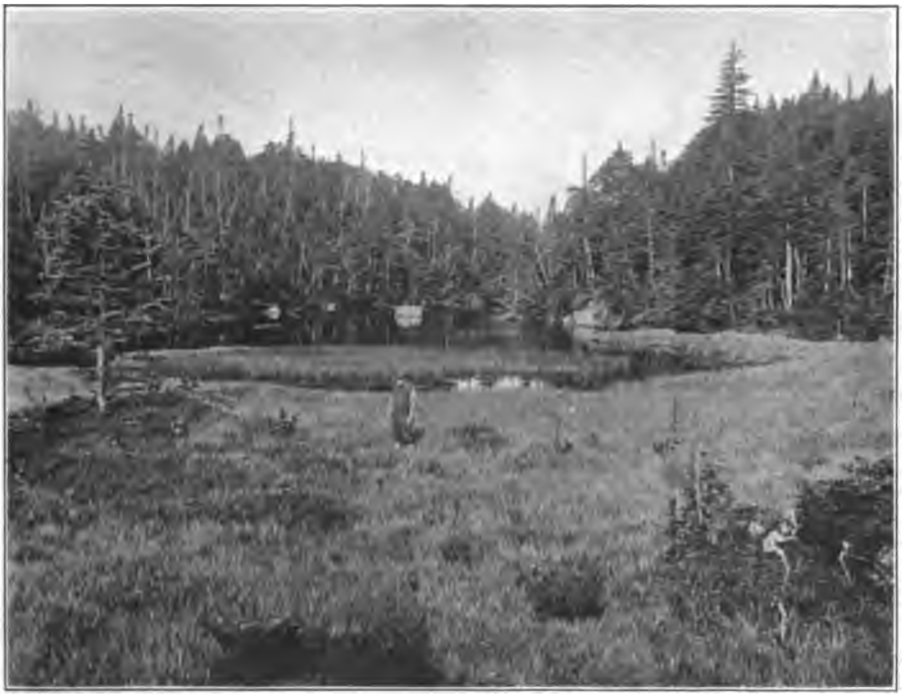

FIG. 5. Lake Tear and the bog, headwaters of the Hudson River, 4,320 feet elevation. Atmometers of station *b* are visible in front of the standing figure.

Stations c 1 and c 2.—These stations were on a shoulder of the mountain in the extreme upper edge of the continuous forest where it reaches timber line. They were in an even stand of fir trees, 7 to 12 feet high, with a maximum breast height diameter of 6 inches, and average of about 3 inches. The tops showed wind damage on the northwest. It seemed best to take records both near the tops of the trees and also under their rather dense crowns. This would give data concerning the conditions under which the

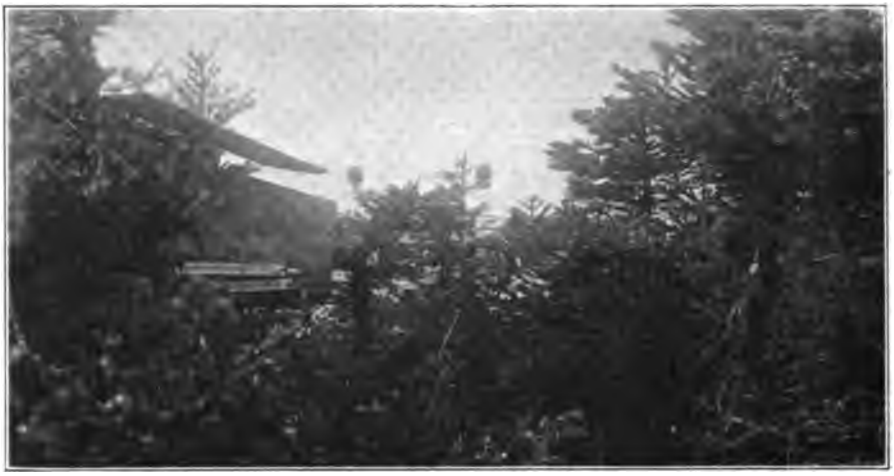

Fig. 6. Station *C1*, showing instruments set in the tops of trees to measure the environment of the forest canopy.

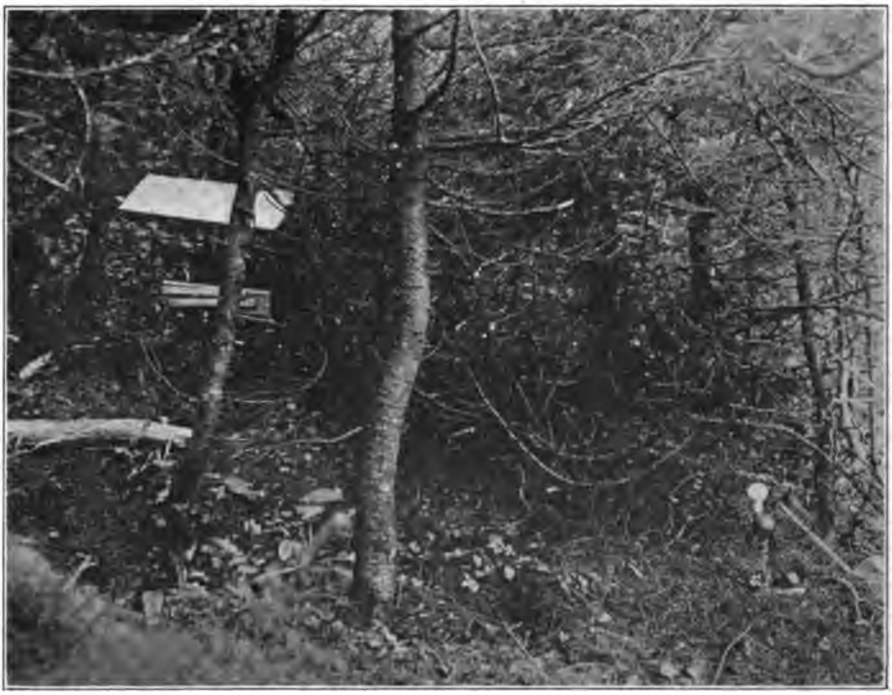

Fig. 7. Station *C2*, showing instruments set under the dense cover of the dwarf fir to measure the environment of the forest floor.

present trees live and an idea of some of the factors influencing natural reproduction. Hence station *c* 1 (fig. 6) and station *c* 2 (fig. 7) were established. In placing the instruments at the former, the tops of trees were removed and the instruments so placed that they were as fully exposed as the tops of the trees had been. The atmometers, especially the white one, could be seen from long distances. The thermometers were located on adjacent trees with similar exposure, care being taken to protect them, however, from the direct rays of the sun. At station *c* 2 the atmometers were placed about 5 inches from the ground, their reservoirs being buried in the heavy covering of moss; the thermometers were attached to trees at about 2 feet above the forest floor. This station was protected from wind, the light was very weak, and the atmosphere was at all times during the study apparently near saturation.

Station d.—This station was located at the lower edge of the alpine vegetation just above the continuous forest. It was on a rock ledge which sloped steeply down to stations *c* 1 and *c* 2, and in one place formed a cliff of about ten feet high. The cliff coincided with timber line. At the station was a layer of peat about four inches thick covered with a dense mat of low shrubs. The atmometers were placed in a north and south line fully exposed. A few yards to the north at the same elevation was a depression in which a few

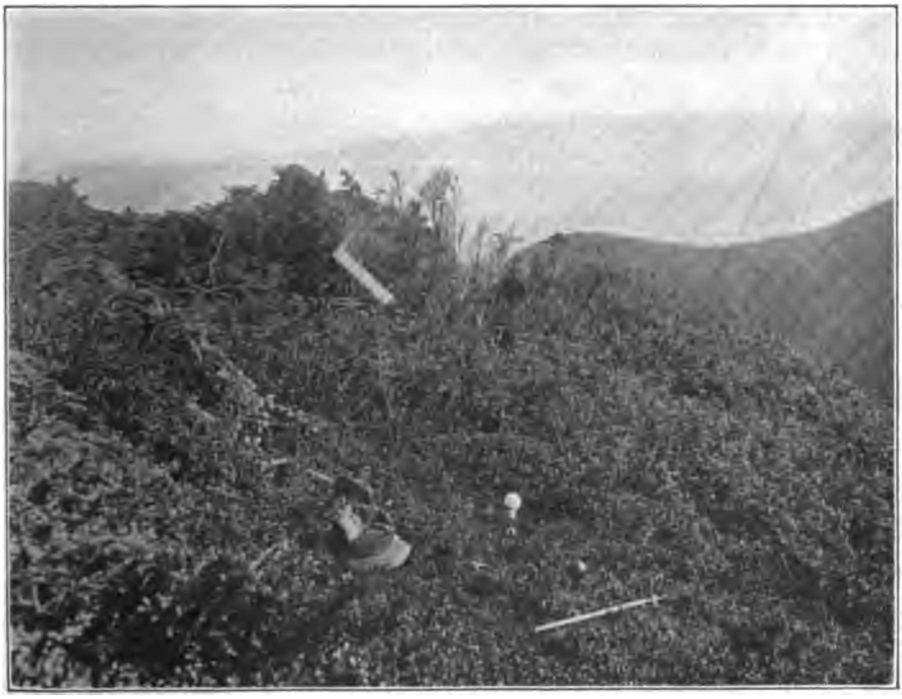

FIG. 8. Station *d* just above timber line, showing atmometers and thermometers.

stunted fir trees reached a height of about 8 feet, their tops extending only a few feet above the general level of the ground. The thermometers, properly protected from the sun, were fastened to one of these trees at about the same elevation as the atmometers (fig. 8).

Evaporation and Solar Radiation.—It was not possible to make readings at such widely distributed stations at 6 A.M. and 6 P.M. as would have been desirable. The readings were taken for the most part between 8 and 9 A.M. and 5 and 6 P.M. They divide the 24 hours roughly into two parts, 10 and 14 hours long respectively, and the graph marked "day" shows the conditions for the shorter period. In the case of the atmometers it was deemed best to add the morning reading to the night reading. This was done because on sunny days the light struck the atmometer a long time before the reading could be made. Very little water evaporated from the bulbs during the night and in fact on rainy nights the reservoir filled so that it was necessary to make the readings from the bottom of the cork stopper instead of from the file mark.

During the first three days of the field study heavy clouds hovered over the mountain tops, and a large part of the time it was raining. The fourth day the sky cleared considerably and the sun appeared. The remaining days were comparatively bright. During the entire period of observation there was a strong wind which was felt especially at the upper stations. The weather conditions did not in all probability differ much from those on Mt. Mansfield in Vermont (elevation 4,075 ft.), where recording instruments were stationed. These instruments show that on the fourth day mentioned above there were only 71 minutes of sunshine, on the succeeding days there were 567, 500, 580, and 60 minutes respectively. The wind movement for these days was 256, 330, 587, 520, and 665 miles respectively. During the night the humidity instrument showed that the air was saturated while during the day the humidity was never lower than 50 percent. These data are shown in figure 9.

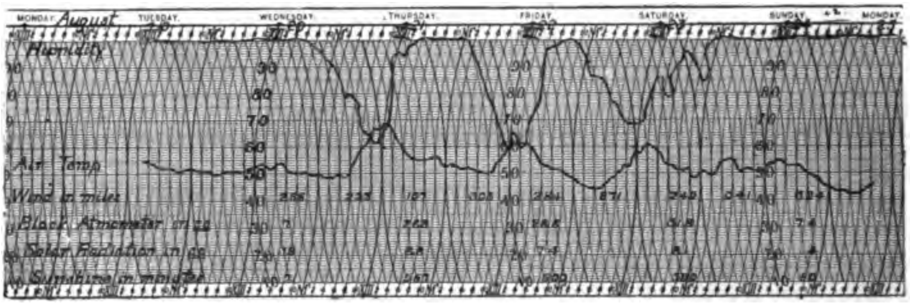

Fig. 9. Weather conditions on Mt. Mansfield, Vermont, August 19 to 25, 1919.

TABLE I. *Evaporation and solar radiation data collected on Mt. Marcy*
Corrected readings of the atmometers and solar radiation expressed in cc.

	Date				
	Aug. 20	Aug. 21	Aug. 22	Aug. 23	Aug. 24
Station *a*:					
Black Atmometer	2.3	16.5	13.5	19.	1.8
White Atmometer	1.5	8.4	6.1	10.3	.7
Solar radiation	.8	8.1	7.4	8.7	1.1
Station *b*:					
Black Atmometer	11.1	20.7	20.6	29.4	5.4
White Atmometer	4.	7.6	9.3	14.6	1.7
Solar radiation	7.1	13.1	11.3	14.8	3.7
Station *c* 1:					
Black Atmometer	9.1	20.	16.4	27.3	4.9
White Atmometer	3.3	7.4	7.	13.3	2.
Solar radiation	5.8	12.6	9.4	14.	2.9
Station *c* 2:					
Black Atmometer	0.	3.7	2.1	5.8	3.5
White Atmometer	.5	3.2	1.5	5.4	3.
Solar radiation	0.	.5	.6	.4	.5
Station *d*:					
Black Atmometer	12.9	24.	20.7	36.2	6.6
White Atmometer	5.6	9.7	12.	20.	2.6
Solar radiation	7.3	14.3	8.7	16.2	4.

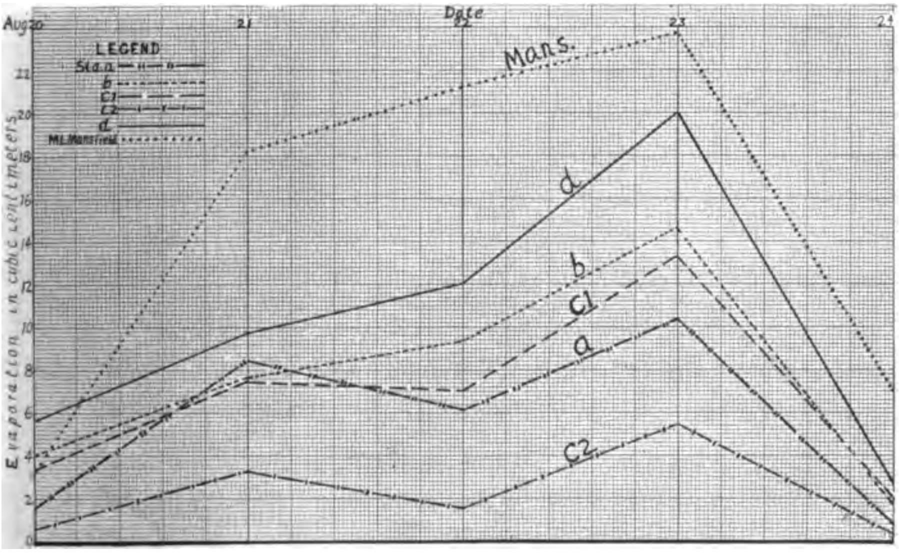

FIG. 10. Evaporation from white spherical atmometers at each station on Mt. Marcy from August 20 to 24, 1919. Evaporation at the summit of Mt. Mansfield, Vermont, is included for comparison.

The corrected readings of the two types of atmometers are given in table 1, and are shown graphically in figures 10, 11 and 12. Figure 10 shows the evaporation from the white atmometers. The highest evaporation occurs above timber line at station *d*, and, except for station *c* 2 which was under the dense fir, and station *c* 1 which will be discussed below, the rate of evaporation shows a tendency to increase with elevation (see also fig. 11).

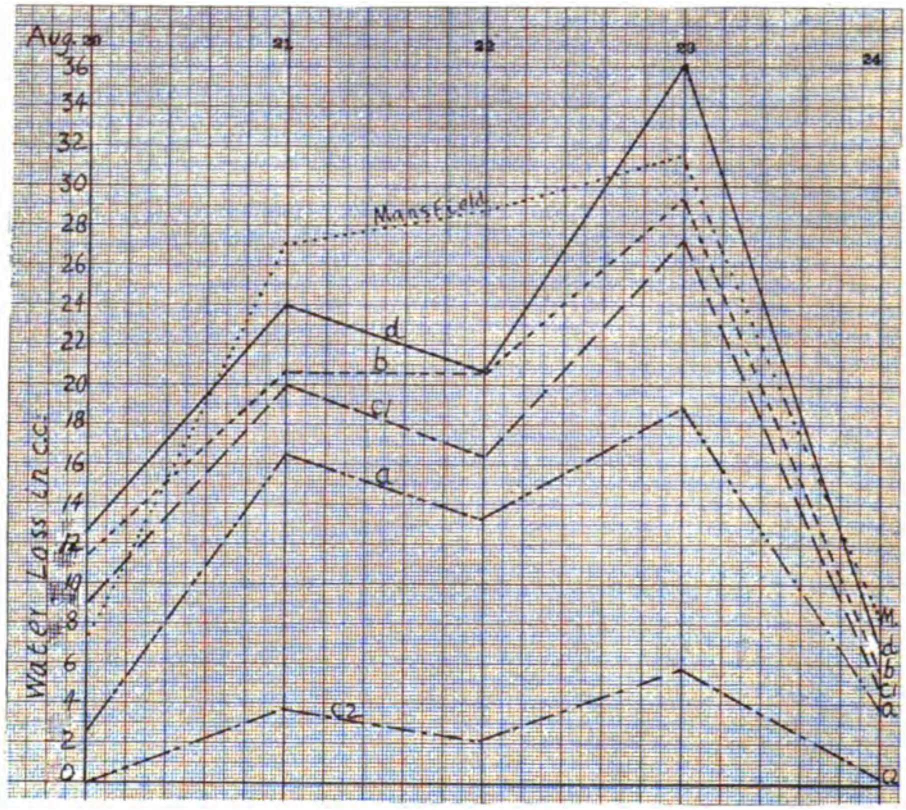

FIG. 11. Water loss from black spherical atmometers at each station on Mt. Marcy, and at the summit of Mt. Mansfield.

The rate in the bog (station *b*) is higher than the rate on the mountain side just below timber line (station *c* 1) in spite of the greater exposure to sun and wind movement at the latter point. This cannot be due to greater cloudiness at station *c* 1, because station *d*, only 75 feet away, showed an even higher evaporation than the bog. It can hardly be due to interception of the wind by the surrounding tree tops because the atmometers were placed above the shelter of these. The question presents itself as to whether or not the stream of moisture transpired by the trees and drawn upward from the forest floor, which at this time was very wet, can be the cause of the lower evaporating rate just below timber line as compared with that just above and in the bog. The moisture transpired by the trees is in all probability greater than that transpired by the much thinner layer of comparatively xerophytic bog plants; that coming through the forest from below, is also probably greater than that which comes from the sphagnum of the bog. It is therefore not unlikely that the volume of moisture coming up from the forest is enough greater than that rising from the bog to produce the difference in evaporation shown by the instruments.

Figure 11 represents graphically the water loss from the black atmometers. Here again the highest rate occurs just above timber line. The stations arrange themselves in the same order as for the white atmometers except that the rate at the lowest station (*a*) is lower than that at the bog (*b*) throughout.

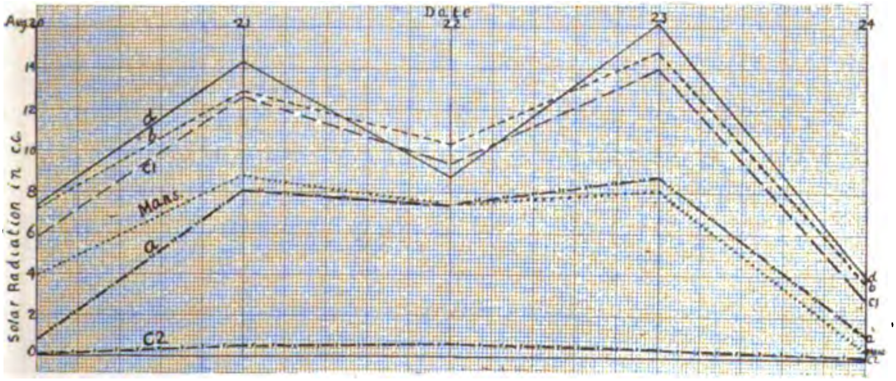

FIG. 12. Solar radiation expressed in cubic centimeters, at each station on Mt. Marcy and at the summit of Mt. Mansfield.

A comparison of the graph representing the rate of evaporation from the top of Mt. Mansfield shows a marked similarity with Mt. Marcy except on August twenty-second when it does not have the dip shown on Marcy.

Figure 12 shows graphically the amount of solar radiation as expressed by the difference between the water loss from the white and black atmometers given in number of cubic centimeters. Solar radiation above timber line was the greatest. If this be taken as 100 percent then the stations arrange themselves as follows: Station *d*, 100 percent; Station *b*, 99 percent; station *c* 1, 89 percent; station on Mt. Mansfield, 56 percent; station *a*, 51 percent, station *c* 2, 4 percent.

It was observed that at times the sun rays pierced the crowns of the fir trees above *c* 2, and struck the bulbs for a few minutes. This probably accounts for the small amount of solar radiation there. In a similar station on Mt. Mansfield during this same period no solar radiation was recorded. Although the fir seedlings have excellent moisture conditions for establishment, as indicated by the low evaporation at station *c* 2, the sunlight which penetrates the dense canopy is insufficient for their development; only when the cover is opened by the death of an old tree can the young trees come up.

The three chief factors which enter into the consideration of the variations recorded above are elevation, clouds and exposure. Station *c* 2, as has been said, was never long subjected to the direct rays of the sun. Station *a* was shaded during part of the day by Mt. Skylight and the vegetation on the mountain side. Local clouds were abundant. At times *d* and *c* 1 were in the clouds while *b* was in the bright sunlight. At other times a heavy mist would cover the atmometers at *b* while the upper stations were in the sunshine.

It is interesting to note that while the water-losses from both the white and black atmometers on Mt. Mansfield at an elevation of 4,075 feet were larger than from any station on Mt. Marcy, the solar radiation was only 56 percent of that above timber line on Marcy.

TEMPERATURE.—The temperature readings are given in table 2, and shown graphically in figures 13 and 14. The variations from day to day were not great at any of the stations, the maxima varying a little more than the minima. The differences in maximum and in minimum temperature between the stations were small.

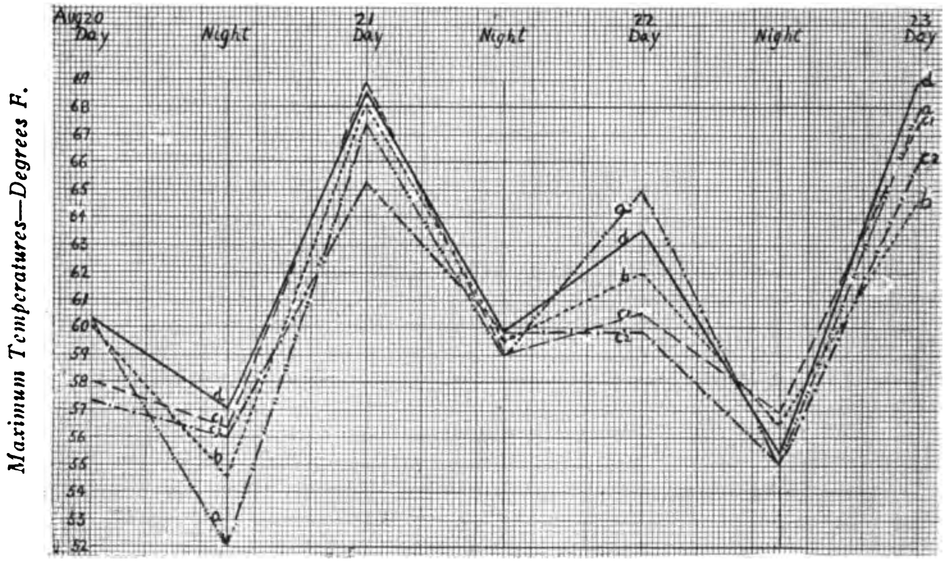

FIG. 13. Maximum temperatures at each station on Mt. Marcy.

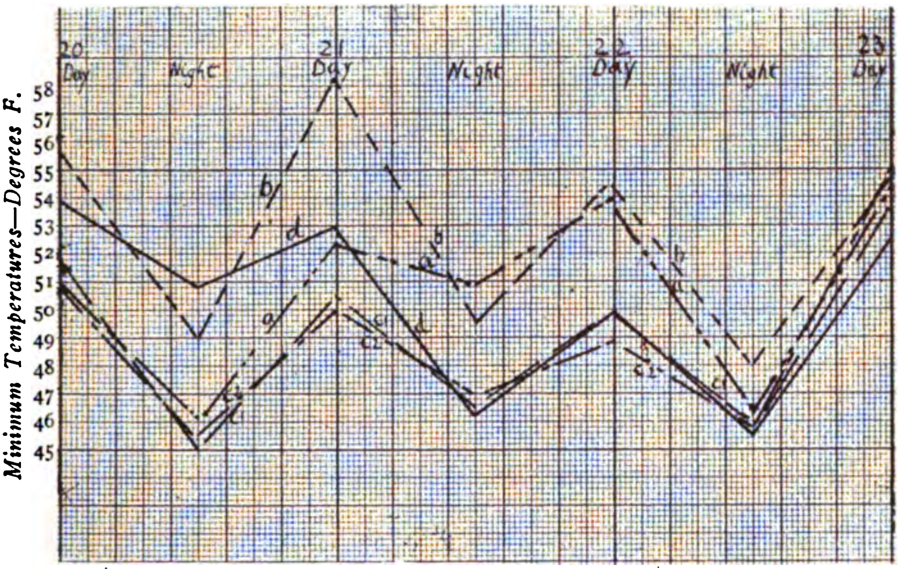

FIG. 14. Minimum temperatures at each station on Mt. Marcy.

TABLE 2. *Temperature readings on Mt. Marcy, August, 1919*

Station	20	21		22		23		24
	Day	Night	Day	Night	Day	Night	Day	Day*
a. Max.	60.3	52.	67.4	59.	65.	55.	67.8	60.9
Min.	51.	46.	52.3	50.9	54.	46.2	54.5	50.
Ave.	55.6	49.	59.9	55.	59.5	50.6	61.7	55.5
b. Max.	60.	54.5	68.	59.5	62.	56.5	64.5	59.7
Min.	55.5	49.	58.2	49.5	54.5	48.	54.8	55.8
Ave.	57.8	51.8	63.1	54.5	58.3	52.3	59.7	57.8
c — 1. Max.	58.	56.3	68.8	59.	60.5	56.9	67.6	58.9
Min.	51.8	45.	50.4	46.5	49.9	45.4	53.5	49.8
Ave.	54.9	50.7	59.6	52.8	55.2	51.1	60.6	54.4
c — 2. Max.	57.3	56.	65.3	59.8	59.9	55.	66.1	58.8
Min.	51.	45.4	50.	46.9	48.8	45.7	51.	49.5
Ave.	54.2	50.7	57.7	53.4	54.4	50.1	58.6	54.2
d. Max.	60.3	57.	68.5	59.8	63.5	55.3	68.9	58.7
Min.	53.8	50.8	53.	46.3	49.8	45.5	52.4	46.9
Ave.	57.	53.9	60.8	53.	56.7	50.4	60.7	52.8

* No night readings for August 23–24.

Bonnier[13] states (p. 336) that the modifications of structure in alpine plants are related to the diurnal range of temperature, which is very low at night and relatively high in the sun during the daytime. Although our thermometers were sheltered from the direct rays of the sun (which gives a smaller range), our results agree in the main with the set of conditions found by Bonnier. The average range of temperature (difference between maximum and minimum) increased with altitude except that the station just below timber line (*c* 1) had a little greater range than just above timber line (*d*). The average ranges, in order of magnitude, are as follows:

Station *c* 1	11.7	degrees F.
Station *c* 2	11.3	" "
Station *d*	10.5	" "
Station *b*	7.4	" "
Station *a*	7.1	" "

Sampson[14] has shown, as a result of studies in the plant zones of the Wasatch Mountains in Utah, that the summation of effective temperatures as proposed by Merriam[15] gives results similar to temperature summations on the physiological basis as devised by Lehenbauer.[16] These summations "have shown much promise in correlating air temperature with physiological plant activities." Summations of our temperature data according to Merriam's method (totals of the mean daily temperature, less 40 degrees) show that the heat available for growth diminishes with increasing altitude, except for the bog at Lake Tear which had the highest effective temperature, due undoubtedly to its longer exposure to the sun as compared with station *a*. Taking the effective temperatures at station *a* as 100 percent, the other stations were as follows:

Station *a*	100	per cent.
Station *b*	105	" "
Station *c* 1	95	" "
Station *c* 2	89	" "
Station *d*	76	" "

It is significant that the greatest change in amount of effective temperatures should occur between the points just below and just above the timber line, in spite of the short distance (hardly 75 feet) between these two points, and that this change should correspond with the abrupt contact between the two life zones. Does not this suggest that the amount of effective temperature may be the leading factor which causes the sharp line of demarkation at timber line?

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[13] Bonnier, Gaston, "Le Monde vegetal" E. Flammarion, Paris, 1914.

[14] Sampson, A. W. "Climate and plant growth in certain vegetative associations," U. S. Dept. Agr. Bul. 700: 1–72. 1918.

[15] Merriam, C. Hart. "Laws of temperature control of the geographic distribution of terrestrial animals and plants," Nat. Geog. Mag., Vol. 6, pp. 229–238, 1894.

[16] Lehenbauer, P. A. "Growth of maize seedlings in relation to temperature," Physiological Researches, Vol. 1, No. 5, pp. 247–288, 1914.

SOIL TEMPERATURE.—The soil at all stations was essentially a bog soil. Analysis shows that its water content varied from 76 percent to 85 percent, of its original weight. As is well known, soils of this nature do not fluctuate much in temperature on account of the great mass of water to be warmed. The readings obtained were:

TABLE 3. *Soil temperature.*

Depth	Stations			
	a	*b*	*c1* and *c2*	*d*
1½ in.	54	58.5	53	55
3 "	52.5	53.5	49.3	50
8 "	—	—	—	47.5
12 "	50	49.5	46.3	—

Temperature in adjacent sandy soils at a depth of one inch were about 20 degrees warmer during the afternoon on sunny days and fluctuated as much as 13 degrees during 24 hours. On one day the maximum soil temperature at this depth was 76 degrees, the minimum, 63°.

SOILS.—Samples of the surface soil were taken in each of the important types of vegetation represented by the stations described above. Since the feeding roots of most plants are close to the surface these samples are fairly representative, although final conclusions would require a larger number, including some of the deeper layers. The mineral soil over most of Mount

TABLE 4. *Soil samples from Mt. Marcy.*

Station	Water, percent	Dry matter, percent	Dry matter contains organic and volatile sub., percent	Ash, percent	Organic and volatile contain nitrogen, percent	Relative lime absorption coefficient	Depth of sample
b	84.79	15.21	12.24	2.97	.312	1	8 in.
b	82.64	17.36	13.40	3.96	.304	1.2	1 ft.
d	76.07	23.93	21.93	2.00	.500	2.2	8 in.
c	80.31	19.69	18.89	.80	.455	2.3	1 ft.
a	81.36	18.64	17.62	1.02	.388	2.1	1 ft.
d	50.75	49.25	17.78	31.46	.389	1.5	8 in.

	100 parts dry matter contain			
	Organic and volatile	Ash	Nitrogen in organic matter	Depth of sample
b	80.47	19.53	2.05	8 in.
b	77.20	22.80	1.75	1 ft.
d	91.63	8.37	2.09	8 in.
c	95.05	4.05	2.31	1 ft.
a	94.53	5.47	2.08	1 ft.
d	36.10	63.90	.79	8 in.

Quality of organic and volatile matter as regards nitrogen is nearly similar. All samples show a large lime absorption coefficient, indicating high acidity.

Marcy is derived from a coarsely crystalline, greenish anorthosite containing approximately ten percent of lime. This rock, even when pounded to powder, gave a hardly perceptible effervesence with hydrochloric acid, but when heated it effervesced strongly.

The analyses of the samples are given in table 4. None except sample 6 contained appreciable quantities of the mineral soil. It is interesting that the mineral soil, even though derived from rock with a marked percentage of lime is nevertheless acid. The analyses indicate that the major differences in the vegetation at the instrumental stations are probably not due to differences in the soil. There are however, examples of plant responses to soil composition as in the case of *Arenaria groenlandica* and *Scirpus caespitosus* which grow on the particles of the rock that do not yet contain sufficient organic matter to become strongly acid. Such a case is noted below under the description of the vegetation of the alpine zone.

The above data probably do not cover a critical period in the conditions of the habitats which were under consideration. At no time were the plants subjected to extreme conditions in light intensity, air or soil temperatures, humidity or soil moisture. Only data collected at such critical periods, that is when one or more of the environmental factors was reduced to its minimum for that habitat, could be used to determine its effect upon plant distribution. That periods exist when conditions are less favorable than they were during our stay was plainly recorded by the vegetation. Although not covering a critical period, the instrumental data indicate certain important differences in the habitats studied, and the authors believe that the collection of this kind of data is valuable in pointing the way to the solution of many problems in plant distribution.

(*To be continued*)

Part II will contain Section IV, the detailed descriptions of the plants and animals on the various habitats mentioned above, and their ecological significance.

Part III will contain the remainder of the paper, including a map and discussion of tree distribution in relation to wind, data on the rate of tree growth above and below timber line, and an analysis of the vegetation in accordance with Raunkiaer's growth forms.

INFLUENCE OF TEMPERATURE AND CONCENTRATION ON THE TOXICITY OF SALTS TO FISHES[1]

EDWIN B. POWERS

INTRODUCTION

The study of ecology involves detailed consideration of the physiological relations of animals to their environments. In many fields accuracy has not been attained. One of these is that of the relation of organisms, especially animals, to salts in soils and water. The lack of accurate means of determining the differences in the relations of different species and of different stages in life histories to salts, etc., has led to much confusion. The prevalence of pollution makes it important to know the relations of fishes to toxic amounts of various salts and other chemicals. Other investigators have shown that different species differ, but the differences were usually merely drawn from general experience. It is the purpose of this paper to show that such difference can be determined with precision. It will also be demonstrated that temperature modifies the effect of a given concentration of a substance according to definite laws, and that a rise of one degree at a high temperature has a much greater effect than at a low temperature. In previous work on the toxicities of certain substances to goldfish, the writer found that their physiological activities with few exceptions follow a general law. The present investigation was undertaken to determine the effect of temperature upon this general law and to correlate this effect with the physiology of the organism.

TOXICITY AND THE MEASUREMENT OF TOXICITY

Toxicity has been variously defined by different workers. A common definition is: Any agent which, when introduced into the animal organism, is capable of producing a morbid, noxious, or deadly effect upon it, is said to be toxic. For the purpose of this paper toxicity will be defined as the effect resulting from any agent, the presence of which causes the death of the fish or interferes adversely in any way with its reproduction, development, growth, or normal metabolism. Up to the present time but very little work has been done in determining in a quantitative way the toxicities of naturally occurring and pollution substances. Shelford (1917) has determined the toxicities of a number of the coal tars and coal tar wastes to certain species of fishes by using the one hour survival time as a criterion. Wells has made a quantitative study of the relations of a number of species of fishes to carbon dioxide, lack of oxygen (1913), salts (1915*a*), and carbon monoxide (1918).

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[1] Contributions from the Zoological Laboratory, University of Illinois, No. 154.

In an earlier piece of work experiments were performed to determine the efficiency of the goldfish as a test animal in physiological assay work (Powers, 1918). In this work, it was found that, as the concentration of a substance was increased, beginning with a very dilute solution, a point was reached at which it was first fatal to fish. This was designated as the threshold of lethality concentration.[2] As the concentration was raised from this point the velocity of fatality, which is the reciprocal of the survival time, rose at first very slowly. This was followed by a more rapid rise, and in turn, at higher concentrations, it was less rapid. There is evidence that at still higher concentrations there was again a more rapid rise in the velocity of fatality. In other words, the ratio of increase in toxicity with a given addition in concentration of a solution, as measured by the survival time of the fish, decreases as the concentration is raised. This decrease in the ratio of increase in toxicity for any given addition in the concentration of the substance tested, is more than sufficient to allow for a constant ratio of increase in toxicity for a given percent addition in concentration of the toxic substance. Thus a sigmoid curve is formed when the velocity of fatality is plotted as ordinate, and the concentration of the substance tested is plotted as abscissa. See curve, *CABG,* figure 1. This curve is taken as a representative of the typical form of curve given by all substances tested both in this, and subsequent work, with the exception of cupric chloride, cadmium chloride, and ferric chloride. The deviation of the velocity of fatality curves of these three salts from the normal was explained in a previous work (Powers, 1918). From a study of the curve *CABG*, fig. 1. is evident that at very low concentrations the upward curvature of the velocity of fatality curve is very small as compared to the increment in concentration of the ammonium chloride. At higher concentrations there is a more rapid upward curvature which finally approaches a straight line. From this portion, *i.e.*, the portion *A* to *B*, the upward curvature becomes less, and the velocity of fatality becomes concave downward. Finally, at very high concentrations, there is again a second phase at which the upward curvature is accelerated. This last point is best shown in the velocity of fatality curve (fig. 2) of the straw-colored minnow (*Notropis blennius* Gir.) when killed in ammonium chloride at 19.8° C., because experiments were run over a much wider range of concentrations than the other series. The velocity of fatality curve, fig. 2, approximates a straight line at 0.017 N to 0.03 N., which is followed by a concave downward curvature from 0.03 N. to about 0.09 N., and by a concave upward curvature from about 0.09 N. to 0.6 N.

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[2] The theoretical threshold of lethality concentration is used in preference to theoretical threshold of toxicity concentration of Powers (1918).

This last point has not been demonstrated for all substances tested, but there is evidence that it holds for all showing the first two characteristics.

In all the velocity of fatality curves studied, there is a portion (*A* to *B*, fig. 1) which approaches a straight line, and, in a criterion for the measure of toxicity, can be considered as a straight line. *AB* (fig. 1) when extended as a straight line cuts the *X*-axis at the point *P*. The concentration of ammonium chloride represented on the scale of the graph by the point *P* has been designated as the theoretical threshold of lethality concentration, and the line *PABF* was called the theoretical velocity of fatality curve. Thus, the slope of the theoretical velocity of fatality curve, or the angle *θ*, fig. 1, can be taken to represent the rapidity with which the rate of velocity of fatality increases with a rise in the concentration of the toxic substance. The theoretical threshold of lethality concentration, and the rate of increase in the velocity of fatality are the reciprocal of each other; *i.e.*, as the theoretical threshold of lethality concentration increases, the toxic activity of the substance can be said to decrease. And when the rate of increase of

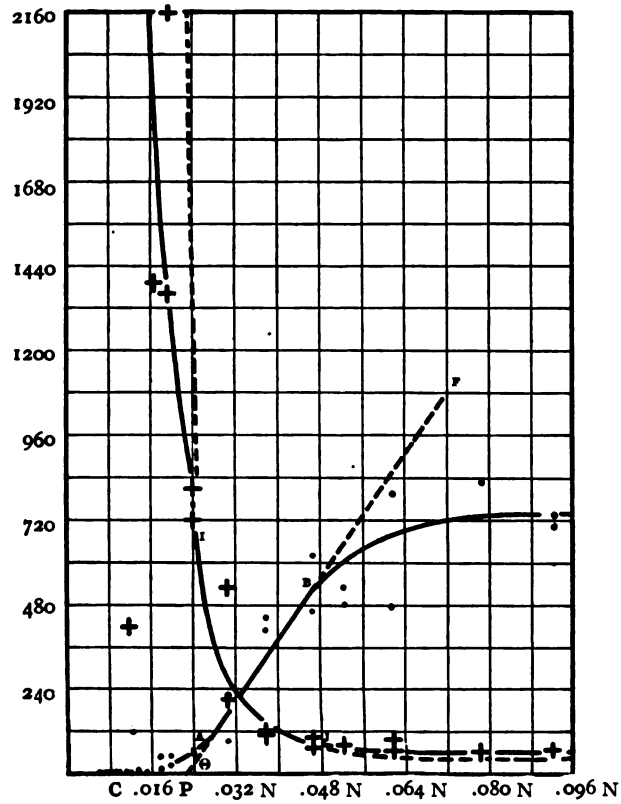

FIG. 1. Relation of concentration of toxic substance to velocity of fatality of goldfish.

velocity of fatality is augmented, the toxic activity can be said to rise. An expression, T (toxicity) $= \sqrt{\frac{\tan\theta}{a}}$, which takes both these factors into consideration has been formulated (Powers, 1918) to express the relative toxicity of a substance. Perhaps a better and more simple expression for the relative toxicity is the equation of the theoretical velocity of fatality curve itself which is the equation of a straight line. That is, $y/(x-a)=K$,

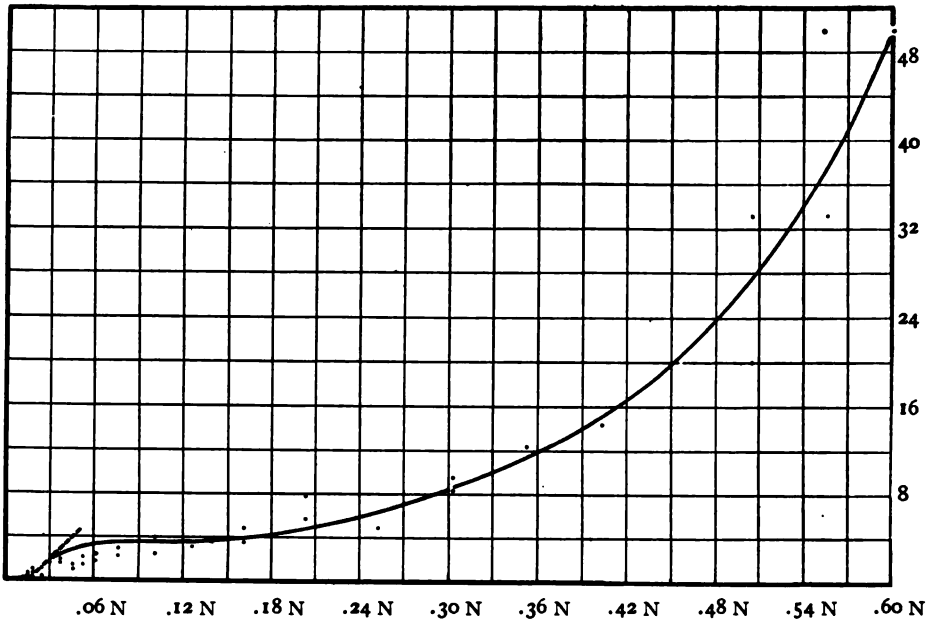

Fig. 2. Velocity of fatality curve.

where y = the velocity of fatality, x = the concentration of the solution tested, and a = the theoretical threshold of lethality concentration. k = a constant and is taken to represent the relative toxicity of the substance.

The equation given above is the equation of a straight line since the theoretical velocity of fatality curve is a straight line (Powers, 1918). The validity of the method is shown by a study of fig. 3. The curves *CABG* and *PABF* represent the velocity of fatality and the theoretical velocity of fatality of the blunt-nosed minnow (*Pimephales notatus* Raf.) when killed in different concentrations of ammonium chloride at 14.2° C., when one block abscissa represents 0.008 N. ammonium chloride; and the curves *C'A'B'G'* and *P'A'B'F'* represent the same data; one block abscissa represents 0.016 N. ammonium chloride. In both sets of curves the ordinate represents velocity of fatality. This is equivalent of having two substances, one of which has iust twice the toxic activity of the other, and in which both follow the same law. It can be proved mathematically that *k* of the equation of the theoretical velocity of fatality curve, *PABF,* and *k'* of the equation of the theoretical velocity of fatality curve, *P'A'B'F'*, show the same relation; *i.e.,* *k* equals one half *k',* and that this relation is not shown by comparing the relative time required to kill the fish in two substances. The same points can be proved when we consider the increased toxic activity of a substance as due to an increased rate of metabolism of the fish, see fig. 4. Figure 4 shows the

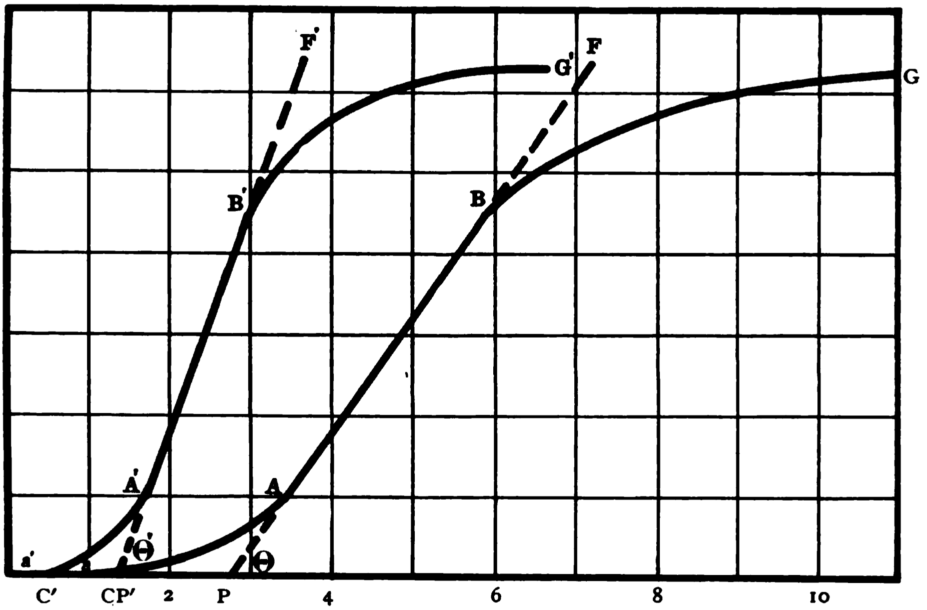

FIG. 3. Velocity of fatality and theoretical velocity of fatality of the blunt-nosed minnow in different concentration of ammonium chloride of 14.2° C.

same velocity of fatality curve, *CABG,* and theoretical velocity of fatality curve *PABF* as in fig. 3, and hypothetical velocity of fatality curve, *CA'B'G'*, and theoretical velocity of fatality curve *PA'B'F'*, in which the effect of the deleterious substance is hypothetically increased by two, due, not to the toxic activity of the substance, but to the increased susceptibility of the fish to the toxic action of the substance as a result of the higher rate of metabolism of the fish. That is, at any concentration of the deleterious substance the velocity of fatality of the fish with the higher rate of metabolism is twice as great as the one with the lower rate of metabolism. This theoretical curve does not hold in its entirety, at least for *Planaria,* as Child (1915 and citations) has shown that at high concentrations of certain toxic substances the *Planaria* with the highest rate of metabolism die first, while at very low concentrations of the toxic substances the order of time until death is reversed. Other factors, such as the size of the individual, the area of surface, the area of the surface of the gills, and the rates of absorption of the deleterious substances, probably play a part. The hypothetical curve can be taken only as illustrating the tendency of the direction of the velocity of fatality curve, when the increase in the velocity of fatality is due to an increased susceptibility of the fish; and shows that the equation of the theoretical velocity of fatality curve can be taken only as a close approximation of relative toxic values. There is some evidence that the velocity of fatality curves of lithium chloride to goldfish at different temperatures do not all meet at the same point on the X-axis. But this is taken as an approximation of the truth and as a method which can be utilized in obtaining a better understanding of the relation of fishes to deleterious substances.

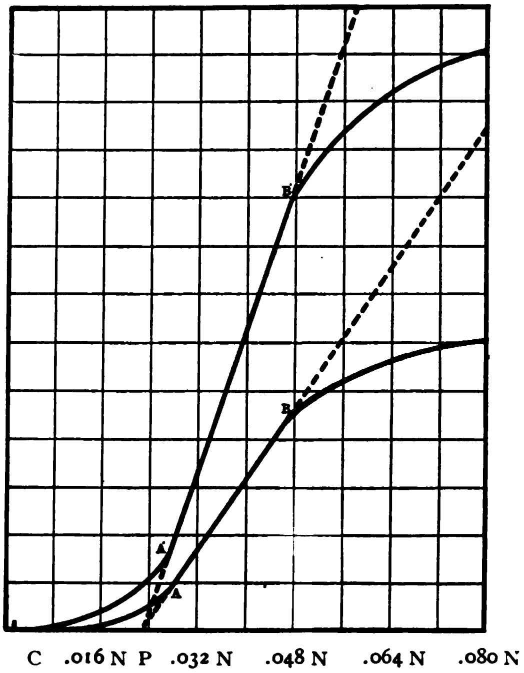

FIG. 4. Same curves as in figure 3, but with effect of the toxic substance increased through higher rate of metabolism of the fish.

METHODS AND MATERIAL

All experiments were performed at controlled temperatures which in no case deviated more than 0.2 to 0.3 of a degree centigrade. These almost uniform temperatures were made possible by the use of a constant temperature bath which consisted of an Alberene stone aquarium 183 cm. by 44.5 cm. by 34.5 cm. deep outside measurements, in which the water stood 15 cm. deep.

The temperature was regulated by the Johnson hot-water thermostat placed at the center of the aquarium. It controlled the flows of hot and cold water which entered the tank at the end opposite the outlet. The temperature of the bath was recorded by a Tycos insertion bulb recording thermometer; it was kept uniform throughout by agitating the water with small widely dispersed bubbles of air.

The fishes to be used in the experiments were kept in running water at a temperature of from 18° to 20° C. The goldfish (*Cerassius cerassius* L.) were obtained of a local dealer and the other fishes were seined from small streams near by. The mortality of the seined fishes was very slight following the second day after they were brought into the laboratory. They were not used in the experiments until the mortality of the stock had ceased, and were rejected after having been kept in the laboratory two or three weeks. In each experiment two fish were placed in 1,500 cc. of a solution contained in a two-quart Mason jar closed with a rubber stopper. The jars were placed in the constant temperature bath and the survival time of each fish recorded.

Distilled water was used in all experiments. This was prepared by condensing through a tube of Jena glass steam from a hot water tank supplied with boiled water. The water when collected was strongly acid from the presence of CO_2, which was removed by aerating with CO_2-free air. After aeration the water gave the following analysis:[1]

Physical examination.			
Turbidity	0		
Color	5		
Odor	2V		
Residue on evaporation.			
Total solids	38	to 42	pts. per million
Alkalinity as calcium carbonte.			
Methyl orange	26	to 36	pts. per million
Chlorides.			
As sodium chloride	0	to 0	pts. per million
Ammonium nitrogen	7.4	to 12.49	pts. per million
Albuminoid ammonia	0.06	to 0.102	pts. per million

This water was not rapidly fatal to fish. Two goldfish lived in it ninety-five and ninety-nine days and six blunt-nosed minnows survived eleven, twelve, thirteen, fifteen, thirty, and thirty-two days respectively. The water was changed every seven days. This specially prepared water was used since it had been found that goldfish would live only three hundred and fifty-two to five hundred and ninety-seven minutes in ordinary distilled water (Powers, 1918).

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[1] Report of Committee on Standard Methods of Water Analysis to the Laboratory of the American Public Health Association, presented at the Havana meeting, Jan. 9, 1905.

EXPLANATION OF EXPERIMENTAL DATA

It has been shown in previous work with goldfish (Powers, 1918) that, when an individual is killed in a toxic substance its survival time is not directly proportional to the concentration of the substance used, but that there is a uniform deviation from this relation which is common to all substances thus far tested, with the exception of the chlorides of some of the heavier metals. Experiments were run with goldfish with lithium chloride, and the blunt-nosed minnow and the straw-colored minnow with ammonium chloride to determine the effect of temperature upon the toxicities of these salts. From these experiments it was hoped to determine the effect of temperature upon rapidity of the toxic action of deleterious substances which might appear in the habitat of the fish either as a natural environmental factor or as a contamination.

In the tables the velocity of fatality which represents the rapidity with which the fish were killed is the reciprocal of the survival time. One hundred, instead of one, over the survival time is used to avoid fractions. The figures are graphic representations of data given in the tables. In all cases the circles (●) and the plus signs (+) represent actual experimental data or calculations made from experimental data.

THE EFFECT OF TEMPERATURE ON THE TOXICITY OF DELETERIOUS SUBSTANCES TO FISHES

(*a*) *The Effect of Temperature on the Toxicity of Lithium Chloride to Goldfish*

A series of experiments was run to determine the effect of temperature on the toxic activity of lithium chloride to goldfish one to two grams in weight. In these experiments the survival time and velocity of fatality of the goldfish was determined over a range of concentrations of lithium chloride from about 0.046 N. to about 0.488 N. between 4° and 34.8° C. at approximately five degree intervals. See table I. By an examination of the data of this table it is seen that, when the survival time or the velocity of fatality of the fish is taken as a criterion for toxicity, the toxic activity of the lithium chloride to the goldfish increases from the lower to the higher temperatures, the greatest increases being at the lowest and highest temperatures. This point will be discussed a little later.

(*b*) *The Effect of Temperature on the Toxicity of Ammonium Chloride to Fishes*

Experiments with ammonium chloride were run with the blunt-nosed minnow at approximately five degree intervals between 14.2° and 24.9° C., and with the straw-colored minnow at 15.6° and 19.8° C. The data on the straw-colored minnow at 19.8° C. is shown graphically in figure 2, lack of space preventing the presentation of this and the other data in tabular form. The velocity of fatality of these fishes was increased with a rise in temperature as was found with the goldfish. The relative increase in the velocity of fatality of the blunt-nosed minnow with rise in temperature will be compared with that of the goldfish a little later.

TABLE I. *Data of goldfish (Carassius carassius L.) when killed in lithium chloride*

Normal	Weight of fish in grams	Survival time of fish in minutes	Velocity of fatality 100/t	Temperature centigrade	Normal	Weight of fish in grams	Survival time of fish in minutes	Velocity of fatality 100/t	Temperature centigrade
0.058	1.6	1411	0.07	4.0°	0.302	1.2	46	2.17	20.0°
"	2.0	1200	0.08	"	"	1.4	46	2.17	"
0.116	1.5	685	0.15	"	0.418	1.2	30	3.33	"
"	1.6	685	0.15	"	"	1.4	31	3.22	"
0.232	1.0	112	0.89	"	0.488	1.6	35	2.81	"
"	1.7	125	0.80	"	"	1.6	35	2.81	"
0.302	1.2	106	0.94	"	0.058	1.0	322	0.31	24.9°
"	2.2	112	0.89	"	"	2.3	466	0.21	"
0.372	1.2	72	1.37	"	0.116	1.3	152	0.66	"
"	1.2	72	1.37	"	"	1.3	157	0.64	"
0.488	1.2	48	2.08	"	0.232	1.3	37	2.73	"
"	1.9	40	2.50	"	"	1.3	38	2.62	"
0.058	1.8	526	0.19	11.8°	0.302	1.5	27	3.72	"
"	1.8	800	0.12	"	"	2.3	36	2.79	"
0.116	2.8	359	0.28	"	0.372	1.1	23	4.34	"
"	2.8	369	0.27	"	"	2.1	25	4.00	"
0.232	1.7	131	0.76	"	0.046	0.9	224	0.45	29.8°
"	1.7	131	0.76	"	"	1.4	244	0.41	"
0.302	1.2	82	1.22	"	0.058	1.3	224	0.45	"
"	1.9	74	1.35	"	"	1.5	263	0.38	"
0.372	1.9	64	1.59	"	0.093	1.1	98	1.02	"
"	2.1	69	1.45	"	"	1.6	98	1.02	"
0.488	1.6	42	2.35	"	0.116	1.1	110	0.91	"
"	1.9	45	2.22	"	"	1.6	124	0.81	"
0.058	1.5	524	0.19	15.3°	0.151	1.1	44	2.27	"
"	1.5	702	0.14	"	"	1.4	49	2.02	"
0.116	1.7	457	0.22	"	0.232	1.1	25	4.00	"
"	2.3	413	0.24	"	"	2.0	36	2.78	"
0.232	1.2	61	1.64	"	0.267	1.2	19	5.26	"
"	2.2	87	1.15	"	"	1.4	16	6.25	"
0.302	1.0	58	1.72	"	0.302	1.0	22	4.55	"
"	1.0	58	1.72	"	"	2.0	36	2.78	"
0.372	1.1	49	2.04	"	0.337	1.1	14	7.14	"
"	1.2	34	2.91	"	"	1.6	17	5.88	"
0.046	1.0	544	0.18	20.0°	0.372	1.3	17	5.88	"
0.058	1.4	410	0.24	"	"	2.3	18	5.56	"
"	1.5	803	0.12	"	0.488	1.3	10	10.00	"
0.093	1.1	152	0.65	"	0.046	1.4	17	5.88	34.8°
"	2.7	213	0.47	"	"	1.7	50	2.00	"
0.116	1.3	192	0.52	"	0.058	1.3	32	3.63	"
"	1.3	255	0.39	"	"	1.3	41	2.42	"
0.151	1.2	75	1.34	"	0.116	1.2	37	2.73	"
"	1.2	80	1.25	"	"	1.4	61	1.64	"
0.232	0.9	57	1.76	"	0.232	1.1	10	10.00	"
"	1.4	81	1.23	"	"	1.3	15	6.67	"
"	1.0	35	2.86	"	0.302	1.0	8	12.50	"
"	1.0	36	2.78	"	"	1.9	8	12.50	"
0.267	1.4	34	2.94	"	0.372	1.3	7	14.28	"
"	1.4	35	2.86	"	"	1.7	8	12.50	"

(*c*) *The Relation of the Effect of Temperature on the Toxicity of Lithium and Ammonium Chlorides to Fishes and van't Hoff's Rule*

When the data of table I are examined in the light of van't Hoff's rule it is found that, if the actual survival time or the velocity of fatality of the goldfish is taken as a criterion, the ratio of increase in toxicity of the lithium chloride for each approximate rise of ten degrees centigrade gradually increases from the lowest to the highest temperatures tested. Table II gives the ratios for the different concentrations with averages for each approximate ten-degree temperature interval. The temperature interval, 11.8° to 20° C. shows a high average ratio. This is due to individual variation of the fish and to the fact that very exact relative toxicities cannot be deter-

TABLE II. *The ratio of increase in toxicity of lithium chloride to goldfish* (*Carassius carassius L.*) *with an increase of approximately 10 degrees Centigrade*

Normal	4.0° to 11.8° C.	4.0° to 15.3° C.	11.8° to 20.0° C.	15.3° to 24.9° C.	20.0° to 29.8° C.	24.9° to 34.8° C.
0.046	—	—	—	—	2.32	—
0.058	1.97	2.15	1.09	1.56	3.53	10.08
0.093	—	—	—	—	1.87	—
0.116	1.73	1.58	1.60	2.85	1.91	3.15
0.151	—	—	—	—	1.67	—
0.232	0.91	1.60	3.69	1.98	1.16	3.00
0.267	—	—	—	—	1.97	—
0.302	1.35	1.88	3.39	1.86	1.59	3.94
0.337	—	—	—	—	1.97	—
0.372	1.08	1.05	—	1.73	—	3.20
0.488	1.04	—	1.24	—	3.50	—
Averages . . .	1.35	1.65	2.20	2.00	2.15	4.67

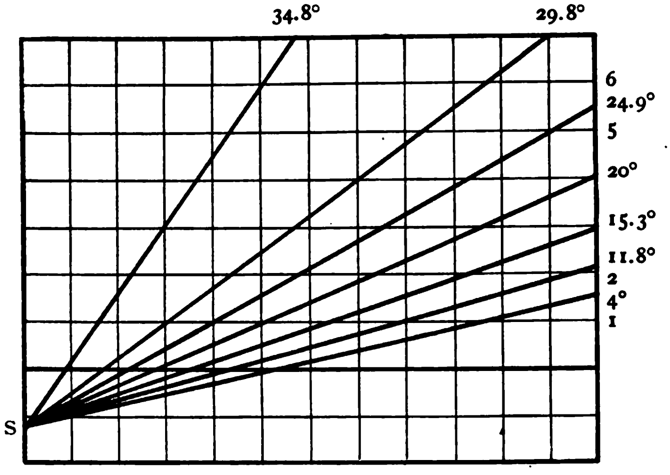

FIG. 5. Theoretical velocity of fatality curves for different temperatures.

mined by comparing the survival time or the velocity of fatality of the fish directly with each other. From this table it is seen that the ratios of the rise of toxic activity of the lithium chloride to the goldfish at lower temperatures is much below and at the higher temperatures is higher than that required by van't Hoff's rule. If the data of table I is plotted in the light of the general relation which the concentration of deleterious substances bears to their toxic activity to fishes, *i.e.*, let the abscissæ represent the concentration of the lithium chloride and the ordinates represent the velocity of fatality of the goldfish and draw the theoretical velocity of fatality curve for each temperature, you obtain the curves shown in figure 5, which is the superposition of the theoretical velocity of fatality curves for each of the temperatures tested. When we determine the relative toxicities of the lithium chloride to goldfish at the different temperatures by means of the equations of the theoretical velocity of fatality curves the individual variations of relative toxicities at different temperatures and the ratio of the increase of toxic activity for a rise of approximately ten degrees centigrade mentioned above disappear to a greater extent. Table III gives the results of these calculations. These results still point to the fact that the ratio of increase in the toxic activity of the lithium chloride for a rise of approximately ten degrees centigrade is much lower at the lower temperatures than that required by van't Hoff's rule. If the data given in column 2 of table III are plotted, a curve can be drawn as shown in *A* of figure 6. This curve has been designated as the temperature toxicity curve. When the Q_{10} is calculated for all the temperatures from 4° to 34° C. on the basis of the toxicity temperature curve (*A* in figure 6) the results given in table IV are obtained. From this table it is plainly seen that the Q_{10} does not meet the demand of van't Hoff's rule, *i.e.*, fall within the limits of 2 to 3, except at the higher temperatures, but that there is a gradual increase of the Q_{10} from the lowest to the highest temperatures, with the greatest increase at the lower and the higher temperatures.

TABLE III. *The relative toxic activities of lithium chloride to the goldfish (Carassius carassius L.) at different temperatures when determined by the equations of the theoretical velocity of fatality curves*

The ratios of increase in the toxicity of the lithium chloride for an approximate rise of ten degrees Centigrade at different temperatures are also given.

Temperature centigrade	Relative toxic activity	Temperatures compared	Ratio of increase in toxity
4°	1.58	4°–15.3°	1.52
11.8°	1.93	11.8°–20°	1.61 −
15.3°	2.40	15.3°–24.9°	1.63 +
20°	3.10	20°–29.8°	1.67 +
24.9°	3.92	24.9°–34.8°	2.55 −
29.8°	5.18		
34.8°	9.99		

The data obtained by killing the blunt-nosed minnow in different concentrations of ammonium chloride at 14.2°, 19.8°, and 24.9° C. have been subjected to the same treatment. When the relative toxic activity of the ammonium chloride to the blunt-nosed minnow at the given temperatures are reduced to relative terms of that of the toxic activity of the lithium chloride to the goldfish at different temperatures it is found that the two sets of data conform closely. See the plus signs (+) figure 6.

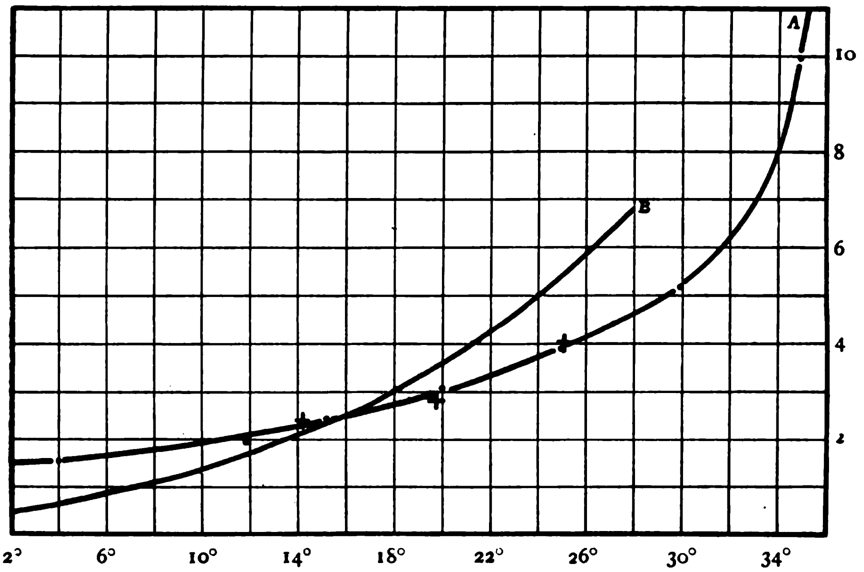

FIG. 6. Temperature toxicity curve (*A*), and Krogh's temperature standard metabolism curve of vertebrates (*B*).

TABLE IV. *The Q_{10} for the toxicity of lithium chloride to goldfish (Carassius carassius L.).*

The calculations are based upon the temperature toxicity curve to goldfish.

Temperatures centigrade	Q_{10}	Temperatures centigrade	Q_{10}
4° to 14°	1.39	16° to 26°	1.67
6° to 16°	1.47	18° to 28°	1.70
8° to 18°	1.53	20° to 30°	1.75
10° to 20°	1.59	22° to 32°	1.90
12° to 22°	1.64	24° to 34°	2.23
14° to 24°	1.66		

A COMPARISON OF THE TEMPERATURE TOXICITY CURVE WITH THE TEMPERATURE METABOLISM AND THE TEMPERATURE STANDARD METABOLISM CURVES OF OTHER WORKERS

When the data of other workers (see Snyder, 1908 and 1911, for a good bibliography of work done up to that time) are examined it is found that there is a great variation in the effect of rise of temperature or the Q_{10} of physiological and metabolic processes when tested over a very wide range of temperatures. Snyder (1911) says, "in fact, the writer knows of no case where this variation does not occur." Blackman (1905) has said, "As regards the rate of metabolic chemical change in the organism at higher temperatures, this law (van't Hoff's rule) clearly does not express the whole truth." As a general rule there is a decrease in the Q_{10} from the lower to the higher temperatures. Krogh (1916) points out that, "when it is attempted to express the temperature variation of the respiratory exchange by means of the rule of van't Hoff, Q_{10} is found to vary greatly, and in the experiments which have given the most uniform results Q_{10} shows a steady and very large decrease with increasing temperature." In other cases (Loeb and Northrop, 1917, Lillie, 1917, and Groves, 1917) there is no tendency for the Q_{10} to decrease at higher temperatures. In certain of these experiments as well as those of the toxic activity of the lithium chloride to the goldfish there is a sharp upward trend of the Q_{10} at the higher temperatures. This greater increase of the Q_{10} at higher temperatures, at least in the case of the toxic activity of the lithium chloride, is possibly due to an additional factor which has reached its higher points of acceleration. That is, the higher temperatures are nearing the upper limits of temperature endurance of the goldfish. A few of the goldfish died in tap water at 34.8° C. and all died when the temperature was raised above 36° C.

Leitch (1916) in attempting to show that Blackman's (1905) method of extrapolation in calculating the effect of temperature on the growth rate of *Pisum sativum* is untenable has compared his rate of growth curve to Krogh's (1914*b*) standard metabolism curve of vertebrates, and claims that the two are in agreement. But when the temperature toxicity curve of the lithium chloride to goldfish is compared with Krogh's temperature standard metabolism curve, it is found that the two do not coincide (*B* in fig. 6), but that the temperature toxicity curve approximates the square root of the temperature standard metabolism curve. The ratio of the square root of Krogh's temperature standard metabolism curve and the temperature toxicity curve shows a slight rise of the latter above that of the former, both at the lower and higher temperatures. On the other hand the data of Loeb and Northrop (1917, tables IX and X) for the reciprocal of the total duration of life and the duration of life of the imago of the fruit-fly conform fairly well with Krogh's (1914*a*, *b*) temperature data for the pupæ of *Tenebrio molitor* when relative values of the two sets of data are compared. There are slight variations at the higher temperatures. Lillie's (1917, tables II and III) data conform less exactly with Krogh's temperature metabolism data and show that the velocity of activation of the starfish eggs is higher at the lower and higher temperatures than the relative rate of metabolism of the pupæ of the meal-worm. Sollman, Mendenhall, Stingel (1915) found that the effect of temperature on the time required for systolic standstill of excised frog's heart injected with ouabain corresponded very nearly to the square of the heart's rate quotient. These workers suggested as an explanation, that, on the basis of Weizsaecker's observations, the activity of ouabain is proportional independently, to two factors, viz., the heart's rate and the temperature. That is, when the temperature and the activity of the heart both varied, the activity of the ouabain would increase by the temperature factor multiplied by the rate factor. And they supposed that the temperature affects the rate of the heart and the ouabain response about equally, and thus the temperature would increase the activity by the square of the temperature quotient. The agreement of Loeb and Northrop's data with the temperature metabolism data of the pupæ of the meal-worm is what one would expect, provided the relative effect of temperature on the metabolism of all invertebrates is the same. This last point has not been demonstrated, but Krogh has suggested its probability. Many insects in the imago stage do not take food. Thus you would expect the duration of life, at least in the imago stage of such insects, to be very closely associated with the rate of metabolism. This point is further emphasized by the fact that Krogh (1914) found that the amount of carbon dioxide given off by the pupæ of the meal-worm during the pupal stage is constant for all temperatures at which development is normal. Again the relation of time required to activate the starfish egg with butyric acid (Lillie, 1917) at different temperatures and the temperature metabolism data agree with expectation. That is, according to the hypothesis suggested by Lillie (1915, 1916), the activation process consists essentially in the production of a definite reaction product designated by him as the activating substance. He has shown that the rate at which the butyric acid takes part in the process of activation is directly proportional to its concentration, and suggests that the interaction has the characteristics of a monomolecular reaction. This being true, the temperature should affect the activating and the metabolic processes alike. Thus, the relative increase in the amount of activating substance would be proportional to the relative increase in the rate of metabolism. But the velocity of activation of the starfish eggs is higher than the rate of metabolism of the pupæ of the meal-worm at both the low and high temperatures. This might be explained by the fact that, as Lillie has pointed out, there is a marked activating effect on the eggs at temperatures below 8° and above 28° C. This possibility will account for the higher rates of activation at these temperatures. The fact that the effect of temperature on the toxic activity of lithium chloride to the goldfish follows a curve which is the square root of the temperature standard metabolism curve of vertebrates might be explained on the ground that the lithium chloride attacks some intermediary substance of metabolism. Burge, Neill, and Ashman (1918) have shown that chloroform, ether, magnesium sulphate, and certain other substances attack the catalase of the blood of the cat, dog, and rabbit given these substances. Thus, in this case, one is dealing with the effect of a substance the value of which is equal to the substance introduced. In the case of the starfish eggs, the amount of activating substance that is formed is determined by the rate at which the butyric acid acts on the reacting substance in the cell. Thus the effect of the lithium chloride would have to be considered as that of a reacting substance and not as that of the product of a reaction. Hence, from the law of dynamics, when the two reacting substances are affected at the same rate, the effect on the reaction product would be equivalent to the square of the effect on the reacting substances in a dimolecular reaction, or the effect on the rate of activity of the reacting substances, would be the square root of the effect on the rate of production of the reacting product.

Although there is more or less of an agreement between the square root of Krogh's temperature standard metabolism curve and the temperature toxicity curves of lithium chloride and ammonium chloride, the explanation of the effect of temperature in increasing the activity of a protoplasmic poison is no doubt not so simple. Other factors, such as molecular activity, molecular tension, and metabolic and physiological processes, must be taken into consideration. These suggestions have been made only as a working hypothesis.

THE COMPARATIVE RESISTANCE OF CERTAIN SPECIES OF FISHES

The same method that is used to measure the relative toxicity of a substance to fishes can be utilized to determine the relative susceptibility of different species of fishes to a substance. If the relative susceptibility of different species of fishes to any one substance can be taken as the relative susceptibility of the fishes to deleterious substances in general, the relative resistance of the fishes, which is the reciprocal of their susceptibility, can be found. When the equation of the straight line is employed as a criterion for the measurement of the relative susceptibility of fishes to ammonium chloride their relative resistance to this substance is found as follows:

Notropis blennius Gir. (1.5 to 2.0 g.) has a resistance of 1.0
Pimephales notatus Raf. (approximately 2 g.) has a resistance of 1.5
Carassius carassius L. (3.0 to 4.9 g.) has a resistance of 3.0

These calculations are made only for the sizes of fishes mentioned above. The order of the species may not be the same at different stages of the life-history of the fish. This has never been satisfactorily worked out.

GENERAL DISCUSSION

It is well known that bodies of water become uninhabitable for some of the most valuable food fishes, both through natural causes and contamination. Certain investigations indicate that the conditions (Shelford, 1911, 1911*a*) and the reactions of the water (Shelford, 1911*b*, and Wells, 1915, 1915*a*) have more to do in determining the habitability of a body of water for food fishes than other factors, such as the availability of food. Shelford (1911*a*) has shown that fish do not always occur where their natural food is most abundant. It has been shown by reaction experiments (Shelford and Allee, 1913, and Wells, 1915, 1915*a*) that fishes generally avoid injurious substances which they encounter in nature. But the avoidance of injurious substances which do not generally occur under natural conditions is not so marked (Shelford, 1917). In fact, fishes may react positively to such substances.

Liebig's law of minimum, as it is generally stated, "The yield of any crop always depends on the nutritive constituent which is present in minimum amount" (Hooker, 1917), can be applied in a modified form to the habitability of a body of water by fishes; *i.e.*, the presence of any one substance may render a body of water uninhabitable for a species of fish. But as Livingston (1917) has stated, "this principle is still quite incomplete logically and its statement will assuredly become more complex as our science advances." The deleterious effect of a substance may depend on the stage of the life-history of the fish, whether it be the developing egg, a young and rapidly growing fry, or an adult. In any of the free moving stages of the life-history, the effect of the injurious substances may be determined by the physiological state of the fish which will cause it to become more sensitive or less sensitive and thus react more definitely or less definitely to any environmental factor. At all stages of the life-history of a fish a deleterious substance may become injurious more rapidly under one set of conditions than under another; or, under still others, it may not be injurious. One of the environmental factors which determine the rapidity with which a substance becomes fatal is temperature, as has been shown by the foregoing experiments. The temperature effect, however, may not be so simple, since the content of the water itself is determined by the season of the year, temperature, light, etc., and the fishes themselves probably have seasonal variations as mentioned above.

All these facts have an important bearing on the problem dealing with the fish in relation to its environment. It is hoped that similar work will be undertaken with other stages of the life-history of the fish, and also that the most sensitive stage will be determined.

Summary of Conclusions

1. The toxicities of the chlorides of lithium and ammonium to fishes are increased with rise of temperature.

2. The effect of temperature on the toxicities of the chlorides of lithium and ammonium does not follow van't Hoff's rule in its entirety.

3. The relative toxic activities of lithium chloride at different temperatures to the goldfish (*Carassius carassius* L.) follow very closely the square root of relative standard metabolism of the vertebrates as given by Krogh.

4. A close approximation of the relative deleterious effect of noxious substances upon fishes can be determined by comparing the constants of the equation of the theoretical velocity of fatality curves of the fishes when killed in these substances. The relative resistance of fishes to these deleterious substances can be determined by the same method since the resistance of the fishes is the reciprocal of the deleterious effect of the substance on the fishes.

5. The relative resistance of *Carassius carassius* L., *Pimephales notatus* Raf., and *Notropis blennius* Gir., to ammonium chloride decreases in the order given.

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THE EFFECT OF TWO SOIL TEMPERATURES ON THE YIELD AND WATER RELATIONS OF HEALTHY AND DISEASED BEAN PLANTS

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It has been pointed out in a previous article by the writer[1] that the bean plant infected by the root pathogene, *Fusarium martii phaseoli* varies considerably in its behavior under different conditions. These variations seem to occur even when the amount of infection is the same, and not only in different seasons, but on different fields during the same season. The criterion of the severity of the disease has been the effect on the yield of the crop. Part of this variation has been explained by the writer[1] on the basis of varying amounts of soil moisture. It has been shown that a difference occurred from 30 to 40 percent in the reduction of yield of affected plants on experimental plots during a wet season and a dry season. The inability of the plants with reduced root system to obtain sufficient water to produce pods was the primary cause under these conditions. As the plots were on different fields, other factors not understood might have contributed to this reduction as for example, mineral nutrition, soil temperature, etc. The effect of soil temperature on this disease has been dealt with by Reddick,[2] who has presented data indicating a greater reduction in yield from diseased plants at a soil temperature of 22° C. than at 34° C. No yield was obtained at 15° even on check plants. Reddick pointed out, however, that the uneven rate of growth of the host plants at the different soil temperatures made the data extremely difficult to analyze. Further work is necessary in order to determine correctly the reaction of the affected host plant under these varying conditions. For this reason the present investigation dealing with the water relations of the bean plant and the effect of soil temperature on such plants has been undertaken.

To obtain a clearer understanding of the problem under consideration some of the peculiarities of the disease should be noted first. The dry root-rot caused by *F. martii phaseoli* is mainly a root disease. The fungus never invades the host tissue above ground. Also, unlike many of the species of the genus *Fusarium,* it seldom causes wilt. This has led to the belief that the fungus does not produce substances which when carried to the plant parts above ground, prove toxic enough to cause noticeable injury. The root system of the bean is invaded and becomes dry, leaving only a few surface roots for the plant. As long as there is sufficient moisture in the soil, however, the root stub and these surface roots may supply the plant with enough water to produce a fair set of pods. Under dry conditions, however, the pods are the first parts of infected plants above ground to show injury. They shrivel and become dry. Lutman[8] presents data to show that the concentration of sap is less in bean pods than in any other part of the plant. Since this is the case, it is readily seen that when the plant needs water and is unable to obtain it from the soil in sufficient amounts, it will begin drawing its supply from the pods.

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[1] Burkholder, W. H. The dry root-rot of the bean. Cornell Agr. Exp. Sta. Mem. 26: 1003–1033. 1919.

[2] Reddick, Donald. Effect of soil temperature on the growth of bean plants and on their susceptibility to a root parasite. Am. Jour. of Bot. 4: 513–519. 1917.

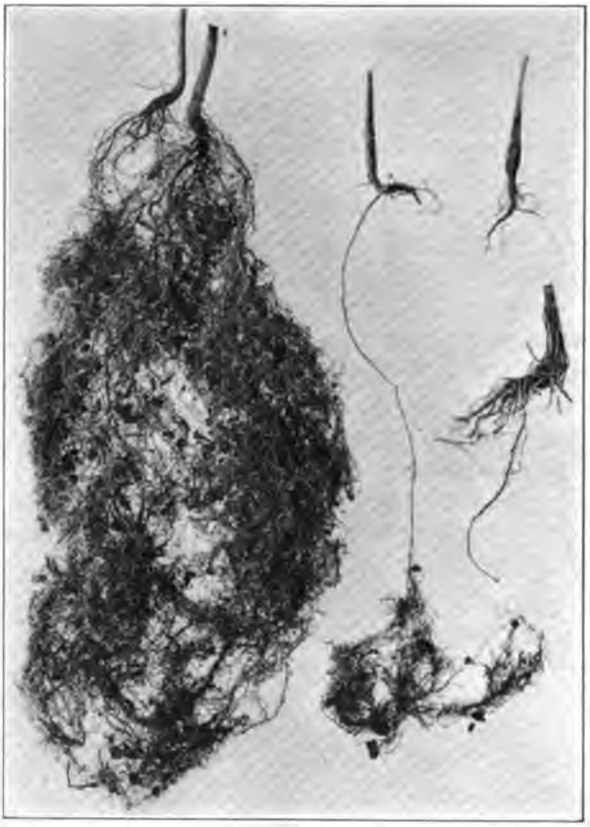

FIG. 1. *Fusarium* root-rot of the bean; showing on the left healthy, and on the right diseased, types of roots occurring in the experiment.

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[8] Lutman, B. F. Osmotic pressure in the potato plant at various stages of growth. Am. Jour. of Bot. 6: 181–202. 1919.

In planning the following experiments especially in reference to soil temperature, the methods employed by Reddick were followed in the main. Some changes, however, suggested by him were used.

Preliminary experiments were begun in the winter of 1918 and the experiments here recorded were conducted in the early months of 1919. Three temperatures were decided upon in these experiments. The lowest was 18° C. and was approximately the temperature of running tap water in the greenhouses during the months the experiments continued. The highest temperature was 33° C., at which beans will grow with little apparent injury, while 26° was chosen as half way between these two temperatures. During the progress of the experiments the plants grown at the highest temperature were killed inadvertently due to a break in the apparatus which raised the temperature for several hours. The data on these plants will not be given, although occasional references will be made to them. Since 18° and 26° C. are near the extremes of soil temperatures found to exist in the bean section of New York State during the growing season of this crop,[4] it is considered worthwhile to give the data on the plants in these two series.

Of the various external factors affecting plants, temperature is the most readily controlled. The temperature of soil in pot cultures has been held uniform in a number of ways,[5] the principles being the same in all cases, the methods varying in detail. In these experiments though a very simple and apparently crude device was used, the soil thermograph records taken throughout show but small variation. These variations were accounted for by temporary disturbances in the supply of electricity, always of short duration and so far as can be seen at present not affecting the results of the experiments in any way. Records for a week at a time do not show fluctuation exceeding 1° C. Galvanized tanks were placed in greenhouse benches with no special insulation, and filled with water. Hot water from a reservoir was let in through a valve which was activated by electricity under thermostatic control. Agitators worked constantly in all pans. The culture vessels used were glazed earthenware jars of one-gallon capacity.

To obtain a cool temperature in one of the pans, a steady stream of tap water was allowed to run through it continuously. During the months of February, March and April when the following experiments were conducted, the temperature of this water varied around 18° C. On a few hot days it rose for a short time to approximately 21° C., and in a few other cases fell to about 15° C. Continuous records were taken of the temperatures in all three pans by the use of Fries' soil thermographs.

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[4] Such records were taken in the bean fields during the seasons of 1916–1919 with continuous self-recording soil thermographs.

[5] Fitch, C. L. Health in potatoes. Colorado Agr. Exp. Sta. Bul. 216: 15–22. 1915.

Jones, L. R. Soil temperature as a factor in phytopathology. Plant World 20: 229–237. 1917.

The soil used to fill the jars was composed of two thirds rich garden loam, and one third sand. It was thoroughly mixed and sterilized before placing in the pots, care being taken to pack it as gently and evenly as possible. The soil moisture was controlled by the use of Livingston auto-irrigators. Two cups were placed in each pot, and the water was retarded by a column of mercury 2 centimeters in height. A bottle with a capacity of five hundred cc. was placed next to each pot, and filled with water from which the auto-irrigators drew their supply. About a week after the bean plants had pushed through the soil, the tops of the pots were sealed to prevent the evaporation of water. Pieces of heavy brown paper were cut to fit the tops, holes being allowed for the bean plants and the tubes of the auto-irrigators. These papers were then dipped into a mixture of hot paraffin and beeswax, and sealed on top of the pots with the same mixture. About the stems of the plants were placed paper tubes to keep the hot paraffin from coming in contact with them. These tubes were plugged with cotton.[6] Thus all the moisture that was lost by the pots was transpired through the leaves of the plants. Each day the amount of water lost from the bottles could be determined and thus the amount of water transpired by the plants in each pot. Tared culture vessels were used so that later in the experiment the soil moisture could be determined approximately by weighing the whole system.

In planting the beans in a glazed pot and covering the surface of the soil with paraffined paper it was possible that a poor aeration of the soil would result and cause injury to the roots of the plants. In the jars in these experiments, it is readily seen that there would be no intake or outflow of air due to fluctuations in temperature. However, the soil in the pots was light and with the use of the auto-irrigators it never became packed. Oxygen is not as essential for the roots of the beans as it is for those of some other plants. This was shown to be true by Noyes, Frost and Yoder[7] where none or but little injury resulted when the soil was saturated with carbon dioxide gas. No injury was noted to the plants in the check pots conducted in the following experiments. A very fibrous root system was produced, but since no unsealed pots were used, its cause could not be attributed to the lack of air.

In order to avoid having a vapor blanket encircle the plants and disturb their transpiration the water bath was covered. This was done by preparing a mixture of melted paraffin and beeswax, and pouring it over the surface of the water. It hardened quickly, and made a very satisfactory covering. It also aided in stabilizing the temperature in all pans surrounding the plants, preventing that in the warmer pans from rising considerably above that in the cooler one. Thus external factors governing transpiration were held as uniform as possible. A white, spherical atmometer, having a coefficient of .89 was run during the entire experiment. The readings of this instrument were made at the same time that the amount of water transpired by each pot was determined. This was between 9:00 and 11:00 o'clock every morning.

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[6] This was done primarily to exclude the fly, *Sciara coprophila* Lintner, the larvae of which cause damage to the roots of beans in the greenhouse.

Hawley, I. M. Jour. Econ. Entomology. June, 1919, p. 271.

[7] Noyes, H. A., Frost, J. L., and Yoder, L. Root variation induced by carbon dioxide gas addition to soil. Bot. Gaz. 66: 364–373. 1918.

The strain of beans used in the experiment was a pure line selected from the variety known as the Well's Red Kidney, and was obtained through the courtesy of G. P. McRostie of the Dept. of Plant Breeding. There were several reasons for using this variety in preference to any other. It frequently has been observed in the field that it is very susceptible to the dry root-rot, and besides, it is much more convenient to handle a bush bean in an experiment of this kind. In using a pure line too, there was less chance of variation in growth among the individual plants.

During the preliminary experiments it was observed that seed placed in a soil temperature of 18° C. germinated very slowly, and further development of the plants was greatly retarded. In the experiments conducted by Reddick, those plants grown at 15° C. were far behind the others and never produced any pods. It is possible that this is due more to a poor germination and start, than to the continuous growth under a low temperature. Bean growers claim that if they obtain a rapid germination and a good growth for the first week or so, they are more certain of a good crop. A number of investigators, too, have shown that any treatment of the bean seeds that affects germination, even advancing it, is liable to react unfavorably on the further growth of the plant. Kidd and West[8] have shown this to be the case when bean seed are soaked in water. For this reason it was thought best to germinate all the seed and grow them for the first week under the same conditions.

Likewise, it has been observed in germinating beans, and especially Red Kidneys that there is frequently a great difference in time of germination not dependent on external factors. For this reason a large number of uniform seeds were selected and put to germinate between moist filter paper. When these began to sprout, the seed coats were carefully removed, and four or five seeds were planted in each pot. After the experiment was under way, the number of plants in each jar was reduced to two. At the time of planting, all pots were inoculated with the nodule organism. Eight pots in each pan also were inoculated with *Fusarium martii phaseoli*. Four pots remained as a check. These beans were planted February 25. Inoculations were made at this time rather than after the jars were placed in their respective water baths for several reasons. When the soil is contaminated with the fungus before planting the seed, infection is more sure to take place than when a suspension of spores is poured about the roots. Infection too, is more likely to be uniform. Furthermore, it had been shown that the soil temperatures to be used did not affect greatly the infecting ability of the pathogene, and the problem was one of influence of soil temperatures on the progress of the disease. The soil temperature during the germination and first week of growth was such as is found in a greenhouse run at temperatures of 70° to 80° F. After the plants had expanded their first true leaves they were then placed in the soil temperatures under which they were to be grown to maturity. This sudden change in root temperature caused a slight flagging of the leaves of the plants at 18° C., but they quickly recovered and showed no other injurious effects. The change was not great for those plants to be grown at 26° C., and as expected, no effect was noticeable. Those plants raised to a soil temperature of 33° C. also showed no injurious effects.

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[8] Kidd, F., and West, C. The effect of soaking seeds in water. The Ann. of Applied Biol. 5: 1–10. 1918.

A more rapid development of the plants grown in the soil temperature of 33° C. occurred than at the two lower temperatures. The foliage was a darker green. Possibly, the nearest to normal growth in comparison with plants grown in the field was obtained in the soil temperature of 26° C. At 18° C. the plants were healthy but grew slowly. Although the different rate of growth in the three pans was very evident, there was not much variation in the blossoming. Beans grown in the soil temperature of 33° C., blossomed March 23 and 24; in soil temperature of 26° C., blossoming occurred from March 24 to 27; while at the lowest temperature, all plants blossomed on March 26 and 27.

On the night of March 23, the accident occurred that killed by high temperatures the roots of the plants grown in the warmest pan. Through this accident some interesting observations were made that have some bearing of the present problem and do not seem out of place here. On the morning of March 24, following the injury of the roots the leaves of the plants were flagging but soon recovered. Transpiration, however, remained normal. On the second day following the accident the transpiration was still approximately normal, but the lower leaves began to turn yellow. This yellowing of the leaves continued, progressing slowly up the plant until the top leaves were finally involved. A defoliation then occurred, followed by a decided drop in transpiration. On March 28, the roots of these plants were examined, and were found to have been killed to the surface of the soil. Between the soil and the paraffin paper the bean stem begun to send out small lateral roots. These were about one cm. or two cms. in length. A few plants that were allowed to remain in the jars soon began to develop new leaves and resume normal growth. From these observations, it seems probable that the dead roots were able to take in water from the soil and send it up to the parts above ground. Normal transpiration was checked only after the substances liberated from the dead tissue began to prove toxic to the leaves. That only a limited amount of the toxin is given off and that it is not continuous may be seen by the fact that the plants were able to recover.

It is possible that when *Fusarium martii phaseoli* attacks the bean root, a similar process occurs. The death of the root tissue is so slow, however, that a sufficient amount of toxin is not liberated to cause a noticeable effect on the leaves. The plant continues an apparently normal growth with the dead root aiding the few surface roots in the intake of water. Only in the decrease of available water supply is there a large decrease in yield.

The growth of the plants in the two remaining pans continued normal until harvest time. Those grown in soil temperature of 26° were somewhat larger than at the lower temperature. The check plants, too, in both pans had a more vigorous growth than the diseased plants, but in some cases, the difference was not readily discernable. No noticeable difference could be observed in the root growth of normal plants in the two series of soil temperatures. In both cases, they were fibrous and filled the pots well. Their weights, however, were not determined. Also no effect of the soil temperatures on the inoculated roots could be observed.

All individuals were harvested at as nearly a uniform state of maturity as possible. This stage was when all pods on a plant had turned yellow. The leaves, too, at this time frequently had all fallen. On the whole, the plants grown in the warmer soil matured earlier, but the difference was not marked. Inoculated plants, too, matured somewhat earlier. At harvest time, determination of the moisture percentage of the soil of each pot was made.

It was the intention of the writer to determine the dry weight of the roots and parts above ground. From this the water requirements of the plants could be calculated. It was more desirable, however, to obtain the weight of the seed, and since the leaves dropped before the seed matured, it was practically impossible to do both. Furthermore, it probably would be unfair to determine the water requirement of the plants based on roots which had partly decayed and fallen off. For these reasons the water requirements used here are based on weight of seed alone.

In table I, the weekly transpiration of these plants has been set forth. In table II, may be found the accumulated results of the experiment. In order to understand these data more thoroughly, certain factors should be explained that no doubt have a disturbing effect on the results. Pots 15 and 29 each had but one plant, so the amount of transpiration and weight of seed should not be compared with the other pots. Pot 14, although a check pot, does not compare favorably with the other checks of that series.

TABLE I. *Weekly Transpiration during Life Period of Healthy and Diseased Bean Plants at Two Soil Temperatures*
Check plants were healthy, others were diseased.

Pot	No. of plants	Mar. 7–13	Mar. 14–20	Mar. 21–7	Mar. 28–Apr. 3	Apr. 4–10	Apr. 11–17	Apr. 18–24	Apr. 25–May 1	May 2–9	May 9–12
Evaporation[1]			75.1	104.7	89.1	87.0	69.1	121.7	100.1	108.6	42.8
Soil Tem. 26°											
13	2	236.3	363.7	451.7	595.3	769.4	647.8	942.0	533.8	332.7	88.0
14, Check	2	119.2	199.0	482.2	592.6	851.7	644.5	1,089.8	793.6	634.3	173.5
15	1	97.5	245.5	563.1	526.8	689.6	512.3	531.3	85.6		
16	2	457.0	483.0	288.8	97.2	9.2					
17	2	332.5	449.6	1,099.5	1,080.3	1,186.5	731.7	861.9	123.4		
18	2	291.6	393.3	317.1	232.5	68.9					
19, Check	2	339.9	536.6	1,284.7	1,296.7	1,563.5	995.5	1,568.5	643.0	90.5	
20	2	295.0	487.8	637.8	814.8	991.2	817.0	1,037.6	816.4	608.0	264.3
21, Check	2	410.1	609.5	1,338.0	1,509.9	1,415.7	1,118.2	1,674.6	1,096.9	485.3	164.2
22	2	136.3	193.7	442.4	499.5	540.2	228.6	74.4	65.4		
23	2	187.5	247.0	596.6	734.7	932.0	627.4	931.6	524.4	45.6	
24, Check	2	221.0	397.3	789.3	1,093.6	1,272.8	921.5	1,395.1	818.5	233.9	
Soil Tem. 18°											
25	2	245.2	365.9	540.7	789.8	919.5	696.3	910.9	628.1	99.2	
26, Check	2	214.1	236.2	518.7	756.4	907.1	707.8	1,110.8	811.4	304.2	
27	2	177.9	186.9	315.4	441.5	586.7	412.0	751.5	609.7	371.3	18.2
28	2	121.5	210.1	231.0	236.2	123.6	53.5	44.4	15.5		
29	1	78.4	153.9	272.3	369.4	250.4	207.2	231.1	204.3	155.6	52.8
30	2	189.1	225.3	346.1	460.1	544.2	512.2	836.7	636.6	398.2	26.5
31, Check	2	227.5	273.2	594.6	674.1	862.3	591.9	1,100.1	808.6	554.3	93.2
32	2	191.6	228.4	233.6	304.4	202.4	105.9	60.9	38.8		
33, Check	2	173.0	251.7	484.5	584.0	726.6	556.1	901.9	808.0	404.4	84.6
34	2	129.7	166.6	246.5	272.9	285.4	221.5	262.2	214.4	38.7	
35	2	131.0	177.2	179.3	249.0	251.9	241.7	379.8	275.8	265.9	116.7
36, Check	2	94.5	195.8	464.6	592.5	673.7	512.3	754.7	532.4	261.9	

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[1] Livingston's White Sphere Atmometer.

This may be accounted for by the fact that it had a very poor start. The auto-irrigator became plugged and the plants suffered from lack of water which caused wilting. Growth from then on was slow in comparison with the other checks. In the last column in table II, the degree of infection for each plant has been recorded. In only about one third of the pots could this be regarded as similar on both plants. The great variation that occurred in the other pots cannot be explained readily by the writer. With so many factors controlled, it was hoped that a greater uniformity would exist. This difference in infection, however, explains some of the irregularities that occurred in the transpiration and in the yield of the plants. Soil moisture determinations were not made until the seed was harvested. At this time all check pots were uniform. The inoculated plants, however, having lost a large percentage of their root system allowed more water to accumulate in their pots. That this accumulation occurred early in the experiment is doubted since other experiments were tested at blossoming time and did not show this to be the case.

The weekly transpiration of the two plants in each pot from the time they expanded their first true leaves, March 7, until harvest, has been recorded in table I. As is to be expected with a more vigorous growth, the transpiration was greater in the series run at 26° C. than in that at 18° C. In both series, however, the rise and fall of daily transpiration followed very closely the rise and fall of evaporation. This also may be seen in the weekly records. The maximum transpiration of all normal plants occurred during the weeks of April 4 and 18. This was the second and fourth week after blossoming. The intervening week between these two periods was characterized by a low evaporation. After the second period of maximum transpiration, the plants began to mature and on this account the use of water dropped off rapidly. When both plants in a pot were severely infected the maximum transpiration occurred at various times. Where there was light infection the course followed somewhat that of the normal plant.

It is probably unfair to average such data as are recorded in table II. The variations explained in a preceding paragraph would not be sufficiently neutralized with the small number of individuals used in these experiments. On the other hand, if differences are large enough no serious objections can be found in considering them in a general way. The following averages in this article apply to single individuals where two were grown in one pot. For this reason, pots 14, 15 and 29 have been eliminated. In soil temperature 26° C. check plants transpired throughout their life period on the average of 4216.0 grams of water, while inoculated plants transpired only 1945.8 grams. Here a reduction of a little over 50 percent took place. In soil temperatures of 18° C., an average transpiration of 2550.4 grams of water took place in normal plants; inoculated plants on the other hand, transpired 1410.6 grams of water. If pot 25 had been eliminated from the averages, a very close approach to a 50 percent reduction would have occurred here also. Pot 25, although one plant showed a severe infection, produced a normal yield of seed and maintained a high transpiration.

TABLE II. *The Effect of Two Soil Temperatures on Healthy and Diseased Bean Plants*

No. of pot	Inoculation	Date of harvest	Total water loss	Weight of seed	Water requirements per gr.	Infection	
						Plant 1	Plant 2
26° C.							
13....		5–11	4,960.7	10.29	482	Severe	Fair
14....	Check	5–12	5,580.4	8.28	673		
15....		4–27	3,251.7	6.10	533	Fair	
16....		4–4	1,335.2	0.0		Severe	Severe
17....		4–27	5,865.4	14.29	410	Fair	Light
18....		4–7	1,303.4	0.0		Severe	Severe
19....	Check	5–3	8,318.9	16.38	507		
20....		5–12	6,769.9	13.65	496	Severe	Light
21....	Check	5–12	9,822.4	14.96	656		
22....		4–30	2,180.5	4.07	535	Severe	Fair
23....		5–3	4,826.8	12.28	393	Severe	Fair
24....	Check	5–8	7,143.0	13.10	545		
18° C.							
25....		5–3	5,195.6	12.18	426	Severe	Light
26....	Check	5–7	5,566.7	14.16	393		
27....		5–7	3,871.1	8.87	436	Severe	Light
28....		4–27	1,035.8	0.0		Severe	Severe
29....		5–12	1,975.4	3.32	595	Severe	
30....		5–9	4,175.0	9.98	418	Fair	Light
31....	Check	5–12	5,779.8	11.56	499		
32....		4–30	1,366.0	.15		Severe	Severe
33....	Check	5–12	4,974.8	9.41	528		
34....		5–5	1,837.9	3.45	532	Severe	Fair
35....		5–12	2,268.3	4.00	567	Severe	Severe
36....	Check	5–8	4,082.4	12.10	337	Very light	

The yield of each pot also has been tabulated in table II. As is to be expected where the soil fertility was held constant there is a correlation between the yields and the amount of water used by the plants. A reduction of about 50 percent in yield is obtained in inoculated plants when the weights of seeds are averaged in the same manner as the amounts of transpiration was averaged. Pot 25, however, still disturbs a close approximation to the 50 percent reduction at the lower temperatures. In the series of plants kept at soil temperature 18° C. check plants gave an average yield of 5.9 grams of seed while diseased plants yielded but 2.75 grams. In soil temperature 26° C. a similar reaction took place. The average yield of the normal plant was 7.40 grams; inoculated plants averaged 3.89 grams. From these data, it appears that the soil temperatures used have very little effect on the disease, at least when the transpiration and yield are taken as the criteria. The temperatures used, as stated above were near the extremes of the soil temperatures found to occur during the growing season in the bean section of New York state. These records were taken for five consecutive years in this section. It may be concluded that the high and low soil temperatures have none or but little effect on the severity of the *Fusarium* root-rot.

The data, on the other hand, show that a low soil temperature decreases the yield of the healthy bean plant considerably. That is, 18° C. shows a decrease from 26° C. Reddick's data show an increase in yield at 22° C. over 34° C. From this the optimum soil temperature for beans can only be guessed at as about 22° C. and 26° C.

It might be wondered at here why a 50 percent reduction both in yields and transpiration occurred in these experiments when the writer has pointed out in the article mentioned before that only a slight reduction in yield occurs on inoculated plants when a sufficient amount of water is available in the soil. It is probable that a sufficient amount of water was available in these experiments. On the other hand, the plants were growing under abnormal conditions and did not as in the field produce numerous surface roots. This fact is possibly the principal cause of the low yields under these conditions.

The "water requirements" recorded in table II are based on the weight of the seed. Considerable variation is found to occur among them which possibly is to be expected since so many different conditions occurred among the plants. The figures, on the whole, appear to be somewhat higher in the 18° C. series. Very little work has been done on the effect of soil temperatures on water requirements. The work that has, as far as the writer is aware, shows no variation with soil temperatures. In these cases, however, the water requirements were based on dry weight of plants. In the soil temperature of 26° C. the inoculated plants required less water per gram of seed than did the healthy plants. This appears to be reversed in the 18° C. series. Wimmer[9] showed that the water requirements of sugar beets and celery is increased by attacks of parasitic nematodes. The explanation that is offered is that the diseased plants grow more slowly. The data set forth in the present article on water requirements in beans gives indications only as to the effect of the various factors concerned. The data are rather limited and should not be accepted as final.

CORNELL UNIVERSITY, 1920

[9] Wimmer, G. Nach welchen Gesetzen erfolgt die Kaliaufnahme des Pflanzen aus denn Boden? Arbeiten der Deut. Landw.-Gesellschaft. Heft. 143: 169. 1908.

ANATOMICAL REDUCTION IN SOME ALPINE PLANTS[1]

C. C. Forsaith

Research in the stelar anatomy of the higher plants has shown that climatic changes have been instrumental in bringing about modifications in structure which may be interpreted as indicative of phylogenetic importance. Jeffrey (7) has demonstrated that prolonged periods of glaciation during past geological ages have accelerated the pace of evolution and, because of the changes thus produced, new types of woody or herbaceous plants have been brought into existence. It therefore occurred to the writer that the peculiar ecological conditions on high mountains, conditions bearing a close affinity with those in arctic regions, might show evidences of progression or differentiation engendered by the bleak unsheltered surroundings which do not obtain in closely allied species indigenous to the low lands. Studies of the few alpine shrubs listed below have demonstrated that such an environment has played an important rôle in promoting progressive innovations in the woody stem, which may be manifest either as new or augmented tissues necessary for the welfare of the plant, or as a reduction or elimination of structures not as important in the intensified struggle for existence.

The material described in this paper was collected during the latter part of July, 1919, on the Presidential Range in New Hampshire, including the mountains Madison, Adams, and Washington. The species chosen for investigation represent the well-known gnarled and twisted "Krummholz" growth characteristic of alpine regions. The specimens were secured from sheltered pockets on the lower slopes of the cones and near the upper limits of shrubs. The exact locations were as follows: on Mount Madison near the Appalachian Mountain Club huts at an elevation of 4,825 feet above sea level, on Mount Adams near Edmund's Col at an elevation of 4,930 feet, and on Mount Washington on Biglow's Lawn at an elevation of about 5,500 feet. The topography at these stations presents steep slopes, composed of broken and only slightly decayed Devonian granite. Scattered among the boulders, there are occasional patches of thin acid soil which furnish a precarious footing for the few sedges, heaths, willows, conifers, and the like which are able to exist under the antagonistic, edaphic, and climatic conditions. In general on the sides of the cones it is possible for vegetation other than lichens to maintain a grip on the rocks only in the shelter of some protecting boulder or in some slight depression. Only in such places

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[1] Contribution from the Department of Wood Technology, The New York State College of Forestry at Syracuse, N. Y.

are plants able to find a refuge from the winds and to secure moisture sufficient for their needs.

The high acidity and sterility of the soil has been caused in large part by water which, leaching through from the upper slopes, has carried away the constituents normally present in other soils. In addition to such a diminution of the organic content, the water has washed away much of the inorganic substance so that plants are often forced to live practically upon bare rock, or at best upon a thin stratum of coarse earth.

Besides a poverty-stricken soil, the alpine plants must contend with the rigors of an arctic climate, and since the anatomical modifications manifest in the stem structure are so intimately related to the meteorology of the region, it seems advisable to treat this phase of the problem in some detail. Beginning with 1872 the United States War Department, Branch of the Signal Service, maintained a station on the summit of Mount Washington, and from their detailed and accurate files, it is possible to secure information as to the prevailing weather conditions for a number of years (8). The annual tabulations demonstrate that variations in the mean from year to year are very slight. The following table represents a summary of the reports from 1875 to 1880. The Fahrenheit scale is used. In the first column is recorded the maximum temperature for each month for the entire period, in the second the minimum, in the third the mean, in the fourth the highest point reached at any one time, and in the fifth the lowest point.

Month	Maximum	Minimum	Mean	High point	Low point
May	39.0	32.4	35.0	62	−1
June	44.9	42.7	44.6	70	15
July	50.4	45.3	48.4	68	31
August	49.1	45.4	47.8	68	26
September	43.5	35.6	39.3	61	11

Such a low average naturally indicates frequent frosts, and a reference to the records shows that no month for the entire period was immunne. For example, frosts were frequent during May, June, and September, and the mercury stood at freezing or below seven times in July and 21 times in August.

Temperature records in so far as they have a bearing upon changes in anatomical structure reach their full significance only as they serve as a basis for comparison. On that account the meteorological conditions prevailing at Burlington, Vermont, a station nearly on the same latitude as Mount Washington but lacking the elevation, furnish some interesting deviations. In the following table, the figures listed for each month represent an average for five years in the respective stations.

	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.	Aver.
Mt. Washington	7	7	13	23	35	45	48	48	39	30	18	10	26.2
Burlington, Vt.	19	23	31	44	59	65	71	69	61	50	37	23	46.4

A study of the above table shows that the difference in temperature is practically 20° F., but of still greater significance is the similarity in the mean obtaining during certain months. To illustrate, the thermal conditions for April on Mount Washington are practically equal to those recorded for February or December in Burlington. In the same way, May is equal to November or March, June to April, July and August to October, September to November, and October to March. It will be observed, therefore, that the degree of heat maintained during the warmer or growing months for alpine plants corresponds quite closely to that experienced by low land vegetation in the same region during April or October, or in other words high altitude species have no summer as the term is understood in the temperate zone.

This difference of 20 degrees Farenheit lends itself to still further analogies. For example, the general range of temperature in semi-tropical Florida is about 72° F., or about 25 degrees higher than listed for Burlington. In the same way the mean recorded for St. Michael, Alaska, is 26° F., or practically equal to that of Mount Washington. It can therefore be assumed that growth in so far as it is influenced by climate is strictly arctic in character,[2] and as different from the surrounding valleys as Florida is from Vermont.

The relative humidity as registered at the base and summit of the mountain shows little variation, and doubtless of itself has little influence in the development of a specialized flora.

In general the barometric pressure shows a difference of about three inches of mercury, or a deviation sufficient to produce a loss in pressure of about a pound per square inch. It is, however, doubtful if this factor has produced any great changes in "Krummholz" shrubs. Such an interpretation is substantiated by the appearance of normal forest trees growing only a short distance below timber line, and by natural forests at even higher elevations in the south and west where temperature conditions are more favorable.

The especially high wind velocities are very important environmental factors affecting the growth of shrubs on exposed mountain slopes. In addition to being intense, the wind comes in gusts, which causes abrupt changes in pressure as well as snapping and twisting strains in the plants. That the wind has caused marked changes in the mechanical anatomy, is well shown by the much thickened patches of fibres appearing at the ends of the annual rings in *Alnus crispa* (Ait.) Pursh. as can be seen by a reference to figure 6, a photomicrograph of a cross section of the stem. That such a division of labor has been brought about by the wind is shown by the absence of similar structures in alders growing in sheltered swamps, and along stream banks.

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[2] [The chief climatic difference would be in the duration of light, which would give longer days in Alaska than on Mt. Washington. Garner and Allard's notable work ("Effect of the Relative Length of Day and Night and Other Factors of the Environment on Growth and Reproduction in Plants," Jour. Agr. Res., Vol. 18, No. 11, March, 1920), which shows the great importance of the relative length of day and night, appeared after this article was written.—EDITOR.]

A little more specific information relative to the intensity of the wind on Mount Washington may not be out of place. During July, 1879 (8), the wind maintained an average velocity of 27 miles an hour with a corresponding force of about 3.6 pounds to the square foot. About the same conditions prevailed during August of that year. In May 1872, the wind reached the velocity of a gale (between 40 and 60 miles an hour with a pressure of 8 to 18 pounds to the foot) at some time during 22 days out of the 31, the intensity of a tornado (60 to 80 miles an hour with a pressure of 18 to 32 pounds), at some time during 16 days, and of a hurricane (80 miles or more with a pressure of more than 32 pounds) during three days. Furthermore, a velocity of 180 miles an hour with a corresponding pressure of 160 pounds is not infrequent. The above records are by no means exceptional or extraordinary, but may be considered more or less normal. High and intermittent strains of this type have engendered modifications in the stem structure as illustrated by the alder. Externally the effect has been in part to develop a very short gnarled stem, as well as diminutive thickened leaves whose duty it is to guard against both laceration and desiccation.

The final factor in the environmental series is rainfall. Although the yearly aggregate is equal to that of any other locality east of the Mississippi and far above the average of 44 inches, very little of the water is available for the use of the alpine plants. Records show that the annual mean is 77 inches, and although this moisture is sufficient in abundance to support a luxuriant vegetation, little can be absorbed owing to a rapid run-off from the steep rocky slopes. So much rain does, nevertheless, exert an influence. On the one hand prolonged cloudy weather minimizes the good effects of an otherwise intense sunlight, but on the other so much water held by the turf below timber line has a tendency to preserve a high humidity and to reduce transpiration.

The various environmental conditions affecting the development of alpine plants may be briefly summarized thus:

1. A thin, sour, poverty-stricken soil.
2. A persistently cold arctic climate with frequent frosts.
3. A growing season similar in temperature to that of spring or fall in the low lands.
4. A high wind velocity producing whipping strains and desiccation.
5. A low barometric pressure increasing transpiration.
6. Steep slopes permitting a rapid run-off of water.
7. Intense sunlight somewhat nullified by cloudy weather.

Just what rôle each of these factors has played in the development of an alpine flora is as yet not fully understood (4). It is obvious, however, that climate has had no small influence as shown by similar external modifications in arctic plants. That a lack of available moisture has been of consequence is attested by cushion plants in arid regions. That high winds have produced modifications is manifest by dwarfed and asymmetrical shrubs on any wind-swept beach. These characters peculiar to alpine plants are doubtless due to an interrelation of all the environmental forces, and a final solution of the part played by each must await still further experimentation. It is not the purpose of the writer therefore, to define just what share each has had in the whole process of specialization, but rather to take the conditions as a whole except in some few cases where modifications are obviously the result of some external influence.

In general the plants indigenous to the upper limits of the Presidential Range show a marked aptitude for a cold, bleak habitat. Many of the species extend northward to the very bases of the perpetual glaciers, and reach their southern boundary in the high altitudes of New England, New York, and in some instances on the more southern peaks of the Appalachians. The above is the general geographical range of the species studied, for example; *Betula glandulosa* Michx., *Betula alba* var. *cordifolia* (Regel.) Fernald, *Alnus crispa* (Ait.) Pursh., and *Rhododendron lapponicum* (L.) Wahlenb.[3]

Such a specialized area as well as one having close affinities with the arctic, has produced many modifications in the stelar structure which appear to have followed the usual evolutionary trend in woody plants. In many instances the adverse ecological conditions have stimulated reduction in certain tissues as will be shown by a study of the species listed.

Turning first to the anatomy of *Betula alba* var. *papyrifera* (Marsh.) Spach., figure 1 shows a transverse section of the normal wood growing in the low lands. Reference to the plate reveals that the vessels are large, diffuse, and evenly scattered throughout the annual ring. The wood parenchyma is abundant, and is arranged in incomplete tangential bands, a feature characteristic of many trees possessing diffuse storage tissue. The wood rays may be included in the diffuse category, and generally vary in width from one to four cells. The prevailing number is three as is shown in the illustration, especially in figure 3. The remainder of the area is occupied by the strengthening fibre tracheids. Figure 3 represents the tangential aspect of the same wood, and shows even more clearly the diffuse and multiseriate character of the rays. Leaving for the moment this valley type which was introduced for purposes of comparison, the structure of the dwarfed alpine birch may be considered. Figure 2 represents a cross section of *Betula glandulosa.* Since the magnification used is 40 diameters greater than that shown in figure 1, the differences in size of the elements engendered by different surroundings may be readily appreciated. As might be expected, the annual increments of growth are exceptionally narrow, and a count showed the average to be about three rings to the millimeter. Those in the paper birch on the other hand, may be as wide as 5 mm. and are rarely less than one. The vessels are about half the size and there is a marked tendency toward their elimination in the outer portion of the summer wood as shown in the central part of the reproduction. The pattern thus produced somewhat resembles that found in *Juglans,* and may be designated as "half ring porus." The most significant departure from the normal forest type appears as a diminution of the width of the ray. Figure 2 demonstrates that the major portion is only one cell in width while very few present more than two cells. Figure 4, a tangential section under the same magnification, reveals this reduced condition in an even more striking way, especially when this figure is compared with figure 3, typifying the rays of the paper birch where no such retrenchment in the storage system has taken place. Around the leaf traces and in regions developed subsequent to injury in *Betula glandulosa,* however, multiseriate rays similar to those appearing normally in *B. alba* var. *papyrifera* are developed as shown in figure 5, a tangential section of the stem including vestigial multiseriate rays. Such a development has doubtless taken place owing to the stimulus produced by a greater abundance of food. Reversion or retention of this type has been mentioned by Bailey (2) thus: "Rapid accumulations of nutritive substances, such as occur in mature twigs of unusual vigor or in regions where traumatic stimulus exists, tend to produce a reversion to ancestral structures."

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[3] Other alpine species showing similar evolutionary tendencies will be described as soon as opportunity to collect the material is afforded.

Hoar (6) has outlined the evolutionary tendencies in the genus *Betula,* and the results of his observations have established the fact that only the diffuse type of ray structure such as that shown in figures 1 and 3 are present in the normal stem of *Betula alba* var. *papyrifera.* His experimental work has furthermore made it clear that this multiseriate ray is not primitive for the paper birch since the aggregate type still persists as a conservative structure in the root, and may be recalled in injured seedlings. In *Betula glandulosa,* however, this archaic storage system does not occur in tissue subsequent to wounding in the first annual ring in so far as could be determined by the material at hand. Furthermore, in the normal stem evidences of more pronounced reduction are manifest in a large number of uniseriate rays. Although the rays thus modified have assumed the form characteristic of the ancient Amentiferæ it does not indicate antiquity in the species, but rather one which has undergone modification and has again assumed the ancestral organization through reduction. Such apparent reversion among advanced members of the catkin bearing Angiosperms is by no means unique as has been shown by Bailey (2). According to this author, the common chestnut shows only uniseriate rays in the mature stem, but the multiseriate form may be retained in recessive regions or may be recalled in response to traumatism. Features like these add strength to the argument that extant members of the Amentiferæ, even though they may closely simulate an earlier phylogenic type have attained such simplicity through reduction from more complicated ancestors. It would appear then that the alpine birch has undergone like modifications in its storage system, and in its present reduced form may be classed as a high type among birches. The stimulus doubtless responsible for such a phenomenon has been a cold climate and an abbreviated growing season.

Betula alba var. *cordifolia* was also examined, but no points of departure from the alpine form already described were noticed. Consequently, any results which may be obtained from studies of *Betula glandulosa* may be applied equally well to the variety of the white birch indigenous to high altitudes.

The genus *Alnus* has been shown to reveal evolutionary tendencies in the Amentiferæ to a marked degree (1, 2, 6 and 7). It has been indicated by the writers mentioned that the uniseriate ray is primitive for the alder. During the evolution of the genus, the uniseriate rays separated only by fibres congregated about the out-going leaf trace, and the congeries thus formed have been classed as aggregate rays. The stimulus thus received from the richer areas about the foliar strands caused this form to persist in the mature wood. This stage is well illustrated by *Alnus incana, rugosa,* and *japonica*. *Alnus acuminata, rubra* and *maritima* have gone even farther in compounding the storage tissue through a transformation of many of the included fibers into parenchyma, so that the resultant structure appears as a collection of multiseriate rays and fibers (1). The same situatian occurs in *Alnus incana* (2) collected from the warmer part of its range where the accumulation of an excess of nutrient matter has been fostered by favorable conditions. In the north a cold climate has prohibited such centralization of carbohydrates so there appears no broadening of the individual rays. The nearly boreal *Alnus mollis* (6) shows still another deviation. Here more frigid surroundings have cut down the materials for conservation, and there has been a concomitant diminution of the storage tissue. In this way the characteristic aggregate ray has disappeared from the mature wood, so that in the normal axis only the uniseriate type appears. Even though such an organization was typical of its ancestors, *Alnus mollis* is none the less progressive, as is shown by the retention of aggregate rays in the first annual ring, root, and leaf trace, and their recall in growth subsequent to injury; thus establishing its advanced position in the genetic scale.

Having outlined the phylogenetic situation in the genus *Alnus,* two species from very different localities may be considered: the first *Alnus* *nitida* Endl., a semi-tropical Himalayan form, and *Alnus crispa,* a dwarfed alpine representative. *Alnus nitida,* the largest of the alders, shows the semi-tropical character of the wood by indistinct limitations of the annual ring. The fibers are large and thick-walled. The vessels are large, evenly distributed, and possess all the features characteristic of the genus. The wood rays as shown in figure 7, a tangential section, are of two types. There are primitive rays, one cell in width evenly scattered between the very large foliar aggregate rays. The large storage areas as can be seen from the print consist of masses of multiseriate rays and fibers. Such an elaboration of the parenchyma tissue might be expected to appear as a result of a warm humid climate where carbohydrate manufacture is sufficient to produce a surplus above the immediate needs of the plant. As in the case of the allied *A. acuminata, rubra* and *maritima* just mentioned, the reserve thus accumulated in *Alnus nitida* has acted as a stimulus for the development of an elaborate storage mechanism. In other words the Himalayan alder appears to have followed the general rule in augmenting the storage tissue under the influence of a warm climate.

In contrast to the situation in *Alnus nitida, Alnus crispa* grows in a cold, bleak, windswept habitat, and the food brought down from the leaves is little in excess of its immediate needs. On this account the mountain alder has found little use for an elaborate storage system, and it would appear that it has consequently eliminated all superfluous tissue. Figure 6 shows in detail a cross section of a normal stem including an end on one annual ring and the beginning of the next. As in the alpine birch, all the elements are small, the pores are diffuse as is also the parenchyma. A significant transformation is obvious in the mechanical tissue which has developed areas of thick-walled fibers at the ends of the annual rings of growth, appearing in the illustration as irregular patches of thick-walled elements. In figure 8 these cells occupy the darker portion of the left-hand side of the figure. Such a feature is more or less unique among alders and doubtless owes its origin to strains engendered by severe wind pressures. The wood ray organization deserves special consideration. As in the northern *Alnus mollis* (6), the aggregate rays have disappeared from the normal stem, so that an examination of the section reveals only the primitive uniseriate type. Figure 8, a tangential section cut from the same specimen, reveals only the evenly separated moniliform lines of cells characteristic of such rays cut transversely. A stimulus retained from the lost aggregate rays appears to persist about the region of the out-going leaf traces, and manifests itself as a prohibition to the formation of the areas of thick-walled fibers as shown in the central part of the figure. In low magnifications, this omission of mechanical tissue shows a very striking likeness to aggregate rays, but a more detailed examination shows that the individual rays are separated by vessels as well as by fibers thus precluding any interpretation as aggregate rays. This situation is well shown in the larger vessels just above the annual ring in the central portion of the reproduction.

It would appear, therefore, that *Alnus crispa,* like *Alnus mollis,* the chestnut, and *Betula glandulosa,* represents a well-advanced member of the genus since it does not build up collections of uniseriate rays about the foliar strands, but has through a reduction of such structures again assumed the aspect of its progenitors. In a genus, then, which is known to be well on the road toward simplification in its evolution, an absence of elaborate tissues would indicate that the mountain alder has gone far in its specialization as a result of a hostile climate, and may to that extent be classed among the high members of the genus *Alnus.*

Rhododendron lapponicum, like the other species, shows evidences of reduction as a result of alpine influences. As in the case of *Alnus* and *Betula* a species from a low altitude is introduced for comparison. Figure 9 shows a tangential section of the deciduous *Rhododendron nudiflorum* (L.) Torr., and the oak-like character of the wood (5) is manifest in the numerous compound rays scattered throughout the stem, three of which are represented in the figure. Between these broad parenchymatous bands, the accompanying primitive rays are evenly distributed, and may be considered as relics of an earlier and simpler form. The other features of the wood are of only passing interest, and since they have no bearing upon the problem will be omitted. The alpine *Rhododendron lapponicum* shows little radical departure except in the organization of the rays, as shown in figure 10 a tangenital section. As in the other examples, the rays show evidences of reduction. In general the broad foliar bands characteristic of the more favored purple azalea have disappeared in the "krummholz" type except in recessive regions. Figure 11 shows a transverse and figure 12 the tangential aspect of the lapland rose bay under a low magnification. As will be observed the growth has been eccentric, and on the narrower side all vestiges of the broad ray have disappeared, leaving only the uniseriate bands. In the wider portion of the stem, however, more rapid growth, resulting from a better supply of carbohydrates, has caused a few of the compound rays to be retained about the leaf traces. On the left-hand side of figure 11, the three dark lines represent broad rays which are in close proximity to a leaf, while on the right, rays accompanying a lower foliar strand appear. That this ancestral hangover is well marked about the foliar region is even better shown in figure 12, a section cut tangentially so as to include the leaf trace and the surrounding tissue. Here the spur of the incoming nutrients has caused the compound ray to be retained even though it has been lost a short distance away. Such a tendency toward reduction in the lapland rose bay may be interpreted as originating from causes similar to those which have fostered reduction in the amentiferous species, and from that standpoint at least, *Rhododendron lapponicum* may be classed among the well-advanced members of its genus.

The three species described in this paper have shown a marked similarity in their development, and consequently one seems justified in assuming that a uniformity of cause has produced like results. All have suffered reduction in the storage tissue, and in addition all seem to have followed the usual trend of evolution in their respective genera. Furthermore, they appear to have progressed farther in many cases than have their low land kin, and may therefore be regarded as high types.

It now remains to enquire a little more closely into the environmental forces which doubtless have been responsible for progression in alpine plants. An arctic climate has, perchance, had more influence than any other factor in bringing about anatomical innovations especially in the tissues reserved for storage. The chief method of control, exerted by temperature, seems to have been as a gauge for metabolism, which in its turn has determined the pace of progression. Physiological studies relative to the effects of heat upon growth (3) have shown that there is a very definite affiliation with the rate of production, and that the rapidity of assimilation of carbon dioxide is practically doubled for every 10° C. within certain limits. A rough comparison of the temperatures prevailing on Mount Washington and Burlington, Vermont, as already listed, shows that according to the above scale assimilation is twice as fast in the low lands as it is in higher altitudes. In the same way it should be four times as fast in a semi-tropical climate such as produced the very broad rays in *Alnus nitida*. It is no small wonder therefore, that an alpine habitat has been the cause of alterations in structure which are generally manifest in the conservation system as shown in the diminution of the ray mechanism in the alpine birch, alder, and lapland rose bay.

That this process of curtailment in the storage tissue is indicative of progress is shown by similar phenomena in closely allied species among the catkin bearing plants as has been shown above. Such an assumption is further strengthened by the retention of broader rays about the conservative leaf trace and traumatic tissue in *Betula cordifolia,* and by the appearance of compound rays in the region of the foliar strands in the alpine rhododendron even after they have disappeared from other portions of the axis.

In contrast to such simplification in plants from high, bleak mountains, *Alnus nitida* shows that a species growing under more beneficial surroundings has had a marked tendency to increase its storage organization in order to conserve the excess of food brought down from the leaves. The much elaborated aggregate rays in the Himalayan alder as illustrated in figure 7, shows that such has been the case, and that semi-tropical surroundings have been instrumental in augmenting the parenchymatous areas.

In contrast to this type of development, a cold hostile climate in alpine regions has through a reduction of the nutrient materials available for growth, forced the plants indigenous to high altitudes to undergo radical changes in the fight for existence. In the light of genetic sequence, therefore, such an evolution may be considered as progressive, and on this account species growing in such regions may be classed as high types among their close kindred living in the more sheltered valleys.

High winds have also been responsible for changes in the mechanical structure, as is shown by the sheaths of much thickened fibers limiting the annual increments of growth in *Alnus crispa*.

In conclusion it may be suggested that climate has played an important part in fostering a progressive evolution in the storage system in plants, that mechanical alterations may be due to the actions of winds or similar tropisms, and that the ecological environment doubtless has a direct bearing upon the problem of descent.

The writer wishes to thank Dr. H. P. Brown, of the Dept. of Wood Technology, New York State College of Forestry, for suggestions.

SUMMARY

It has been recognized for some time by Dr. E. C. Jeffrey and his students that climate has exerted an influence on the evolution of plants. In view of this principle *Betula glandulosa* Michx., *Betula alba* var. *cordifolia* (Regel.), Fernald, *Alnus crispa* (Ait.) Pursh, and *Rhododendron lapponicum* (L.) Wahlenb. were collected from near timber line on the Presidential Range in New Hampshire, examined microscopically, and compared with closely allied species from lower elevations. A marked reduction in the ray storage tissue was manifest in all the specimens. In Betula the major portion of the rays were uniseriate, aggregate rays were not apparent in the normal stem of Alnus, and there was a marked reduction of the compound rays in Rhododendron. Apparently such a diminution of the radial elements had been engendered by the cold, bleak conditions prevailing on mountain tops, where temperature ranges are analogous to those encountered in arctic regions.

The general trend of evolution in the genera mentioned appears to be toward simplification in the rays. Such a marked reduction in alpine species would seem to indicate that hostile surroundings at high altitudes are responsible for a faster progression in the phylogenetic sequence than is manifest in the more sheltered low land species.

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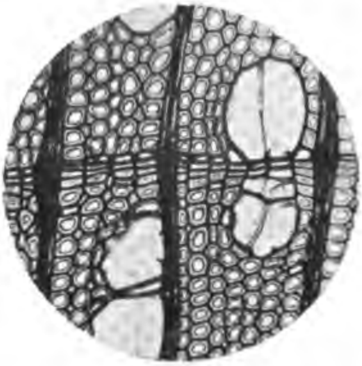
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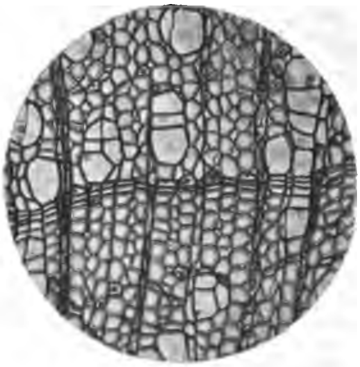
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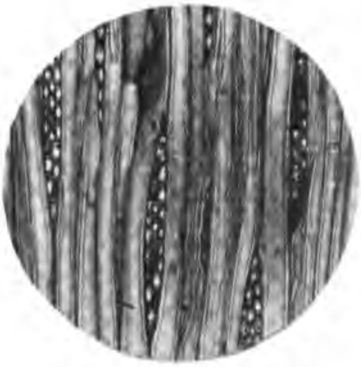
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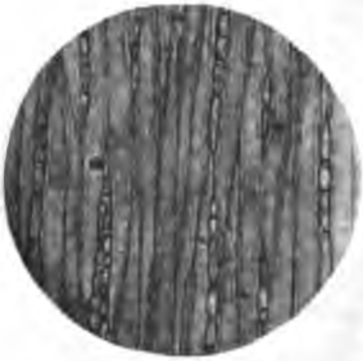
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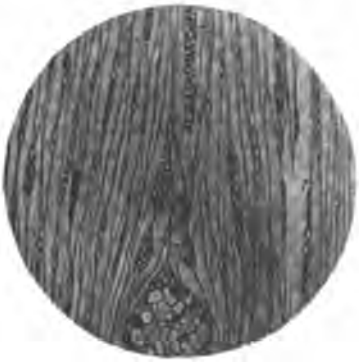
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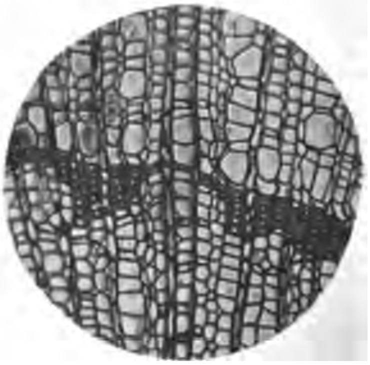
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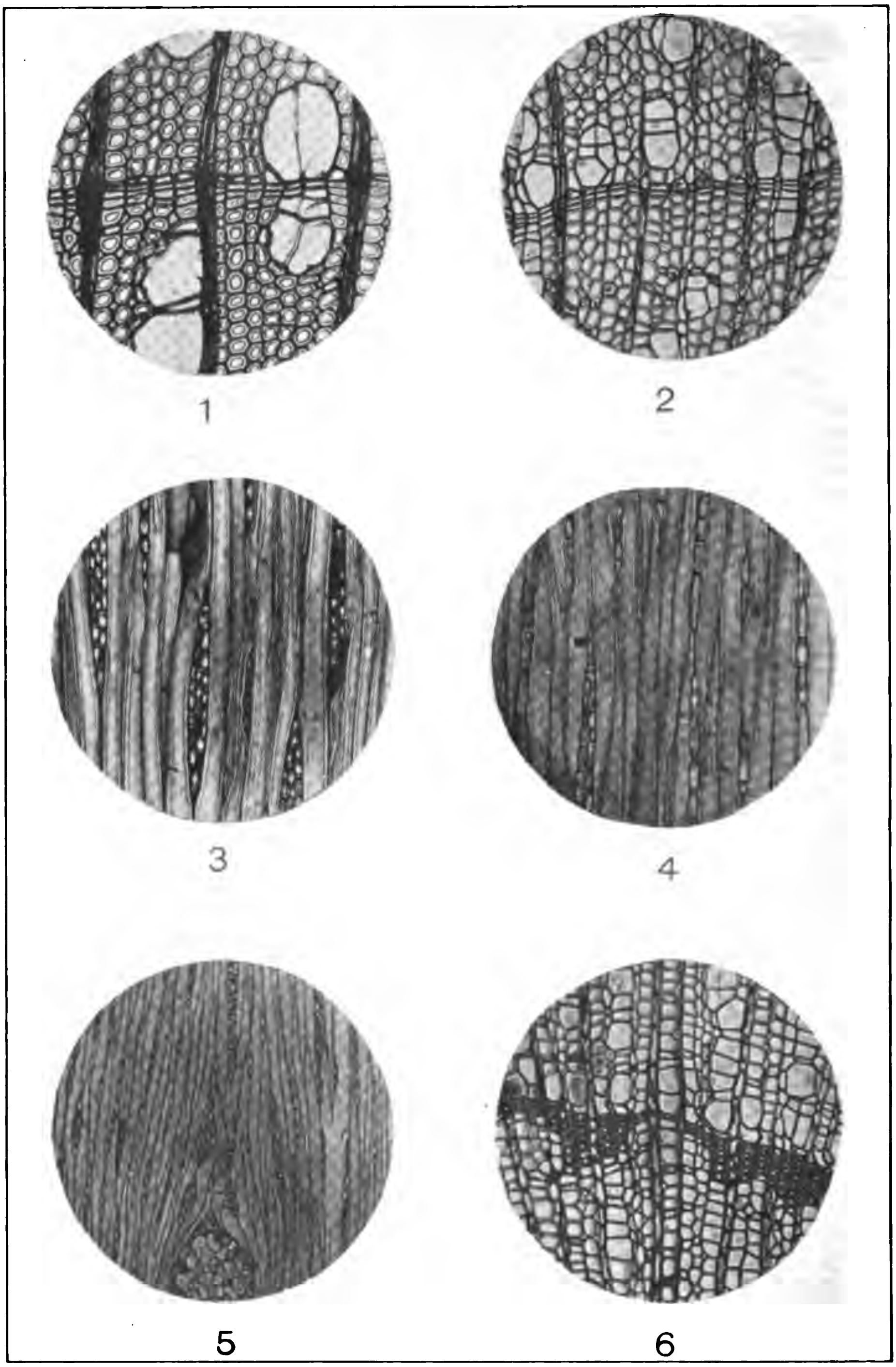

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DESCRIPTION OF FIGURES

1. *Betula alba* var. *papyrifera* (Marsh.) Spach. A transverse section of normal wood showing the multiseriate structure of the diffuse rays. × 160.

2. *Betula glandulosa* Michx. A transverse section of the stem showing reduced rays and half ring porus distribution of the vessels. × 200.

3 *Betula alba* var. *papyrifera*. A tangential section from the same specimen showing diffuse multiseriate rays. × 160.

4. *Betula glandulosa*. A tangential section from the same stem showing predominance of uniseriate rays. × 200.

5. *Betula glandulosa*. A tangential section showing vestigial multiseriate rays. × 80.

6. *Alnus crispa* (Ait.) Pursh. A transverse section including the end of an annual ring, showing uniseriate rays, and much thickened patches of fibers. × 200.

7. *Alnus nitida* Endl. A tangential section of normal wood showing the elaborate aggregate rays and accompanying primitive rays. × 40.

8. *Alnus crispa*. A tangential section of the stem showing uniseriate rays, and thickened fibers. × 200.

9. *Rhodendron nudiflorum* (L.) Torr. A tangential section of the normal stem showing compound and uniseriate rays. × 200.

10. *Rhododendron lapponicum* (L.) Wahlenb. A tangential section of the normal wood showing uniseriate rays. × 200.

11. Same: A transverse section of a stem several years old showing the retention of a few compound rays in the vicinity of the leaf traces. × 20.

12. Same: A tangential section including a leaf strand and showing a few broad rays in its vicinity. Only uniseriate rays appear in the rest of the section. × 40.

NOTES AND COMMENT

At the joint meeting of the American Geographical Society and Association of American Geographers held in New York April 16 and 17, much interesting ecological material was presented. Henry E. Crampton, of Columbia University and the Museum of Natural History, in his paper "The Zoological Facts of Distribution in Relation to the Problem of Subsidence in Polynesia" showed that the snail of the genus *Partula* is confined to those parts of the islands where a comparatively high degree of moisture prevails. Isolation of the islands by subsidence gives an unusually favorable opportunity to study the divergent evolution of the various species in correlation with their insular separation and their further diversification in the suitable ecological situations of the various valleys belonging to one and the same island. Much interesting material on this subject may be found in Crampton's "Studies on Variation, Distribution and Evolution of the Genus Partula; The Species Inhabiting Tahiti," Carnegie Institution of Washington, Publication 228, 1917.

Robert Cushman Murphy of the Brooklyn Museum, in his paper on an "Expedition to the Peruvian Littoral," presented, among other material, a very interesting set of maps showing the control which the cold water of the Humbolt current and of a similar cold current off the coast of southern California exerts upon the distribution of seals, certain fish, and birds which depend upon marine organisms for food.

M. L. Fernald of Harvard, in his paper "The Contrasts in the Geographic Affinities of Certain Mountains on the Gaspé Peninsula" gave striking evidence of the influence of the geological formation upon the distribution of plants. A certain mountain of serpentine containing 40 percent magnesium is so barren that the pictures exhibited might have been taken in the most desert portion of southwestern United States. Yet the precipitation is heavy, and on the amphibolite formation which adjoins the serpentine there is a heavy Canadian forest. "The contact of the two formations could be mapped on snowshoes," said Dr. Fernald. The plants occurring on the serpentine belong to genera which occur most abundantly in the southern hemisphere, while the plants on the limestone formation have arctic affinities. The reason for this has not yet been found.

The Association of American Geographers has adopted the policy of joint meetings with other societies, and has expressed its willingness to hold a joint meeting with the Ecological Society in Chicago next winter. Such a meeting will be of much interest. The tentative arrangements provide for an invitation program of four papers, two by each society.

Ecologists will be interested in the organization of the American Meteorological Society at St. Louis during the meetings at the beginning of the year. The purpose of the Society is to gather into one organization all who are interested not only in meteorology as a physical science, but in climatology and its effects on organic life. While the field of the Meteorological Society does not at all encroach upon that of the Ecological Society, the two supplement each other admirably. Ecologists, no matter in what phase of environment they may be interested, are almost sure to find in the Meteorological Society something of value. At present the dues of the Society are One Dollar ($1.00). It issues a small Bulletin telling of its activities. The Weather Bureau has most courteously placed the Monthly Weather Review at its disposal for the publication of articles, which the Bulletin is not now able to handle. The cosmopolitan character of the Meteorological Society may be judged from its officers: The President is Professor R. DeC. Ward of Harvard, whose main interest is in climate and its effects on man; the Vice-president is Dr. W. J. Humphreys, Professor of Meteorological Physics, Weather Bureau; the Secretary is Dr. Charles F. Brooks of the Weather Bureau, at Washington, Meteorologist and Editor of the Monthly Weather Review; and the Treasurer is Mr. Robert E. Horton, Consulting hydraulic engineer, Voorheesville, N. Y., well-known for his investigations in hydrological meteorology. Among the counsellors are included not only men who are professional meteorologists, but others who are ecologists and interested in the relation of climate to plant life, human diseases and the like, and still others who are particularly interested in the application of weather and climatic studies to business, agriculture and similar activities.

The preservation of adequate natural areas for ecological study is a matter in which the Society is actively concerned and has done much good work through its committee formed for this purpose. Ultimate success in this movement will be of incalculable value to science and will reflect corresponding credit upon the Ecological Society. One of the ways in which the Society can further this matter is by supporting and assisting in every possible way those organizations which have similar aims. The Okefinokee Society, J. F. Wilson, Secretary, Wyacross, Georgia, and the Save the Redwoods League, R. G. Sproul, Secretary-Treasurer, University of California, Berkeley, California, are two such organizations. The former, in the preamble to its constitution states that "its (the Okefinokee Swamp's) great wealth of scenic and scientific virgin attractiveness should be conserved and preserved for public educational, scientific, and recreative uses." The purposes of the Society are:

"First, to secure a part or all of the Okefinokee Swamp as a permanent Government Reservation.

"Second, to cooperate with the government, scientific societies and other agencies in using this reservation as a National History Museum and for a semi-tropical recreation and educational center.

"Third, to give authentic publicity regarding the swamp such as may promise to be of general public and scientific interest."

"The Save the Redwoods League was organized to assist in bringing about a better and more general understanding of the value of the primeval redwood forests of America as natural objects of extraordinary interest as well as of economic importance, and for the purpose of bringing into unity of action all interests concerned with the movement to preserve such portions of these forests as should be saved to represent their fullest beauty and grandeur."

The plans of the League involve:

"1. The securing of a belt of the finest redwood timber bordering the northern highway, in the hope that this area may become a state park.

"2. The obtaining of a considerable body of the most typical primitive redwood forest known, for the purposes of a National Redwood Park."

The League has already secured a number of tracts of forest.

In view of the wide scope of ecology and its importance in the natural sciences and their application, it is desirable that its content be organized and its divisions indicated as definitely as possible.

As a result of the expression of this opinion by a number of members of the society after the St. Louis meeting, President Moore appointed as a committee Professor W. G. Waterman of Northwestern University, Chairman, Dr. J. V. Hofman, U. S. Forest Service, Professor V. E. Shelford of the University of Illinois, and Professor W. C. Allee of Lake Forest University. The purpose in forming this committee was not to establish a system which shall be mandatory, but rather to suggest a classification which is more complete than anything that has heretofore been attempted and which will serve as a step towards a clearer understanding of the subject.

The committee has been working with this purpose in view and has nearly completed a tentative classification which will shortly be submitted for criticism and comment to those of the Society and others who have seemed most interested in the subject; anyone else who wishes to submit suggestions may secure a copy of the classification from Prof. Waterman. When the replies have been received the outline will again be revised and will then be published, probably in Science.

The Cornell Rural School Leaflet, edited by Prof. E. Laurence Palmer, is attempting to approach elementary Nature Study from the ecological view point. The January number contains much of interest to any ecologist. Especially valuable is the life history chart of the mammals of New York. Another issue treating of the ecology of fishes, will appear shortly, and numbers on insects and birds are in preparation.

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The arrangement by which The Plant World is continued under the name *Ecology,* as the official publication of the Ecological Society of America, will not affect the previously existing arrangements for supplying back numbers and sets of the former journal, and the separates and other publications which have recently been offered. It is not possible to supply the first seven volumes. Volumes 10 and 11 can be supplied only in incomplete condition. All other volumes are $2.50 each. Single numbers are 30 cents each. All separates and publications can be supplied at previously advertised prices. A price-list of publications will be sent on application. All paper should be made payable to The Plant World and all orders should be addressed to

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FACTORS CONTROLLING THE DISTRIBUTION OF FOREST TYPES, PART I[1]

G. A. PEARSON

Forest Examiner, Fort Valley Experiment Station

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INTRODUCTION

Every student of plant life in our western mountain regions is familiar with the altitudinal zonation which characterizes the distribution of the forest trees. To the forester this phenomenon is of great significance, since it enables him to determine offhand what species to expect at any altitude on a slope of a given aspect. To the student of problems concerning the growth and perpetuation of forests it affords an excellent opportunity for studying the soil and climatic requirements of different species. The presence or absence of certain species at certain altitudes and slope exposures is immediately associated with temperature, moisture, and other factors prevailing on these sites. It is a matter of common knowledge that as a rule the temperature is lower and the rainfall higher in the mountains than in the valleys below, and therefore it has been assumed that the trees normally occurring at high altitudes have relatively high moisture requirements and low temperature requirements, while those occurring at low altitudes have relatively low moisture requirement and high temperature requirements.

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[1] Based upon Studies in the San Francisco Mountains of Arizona. [The word forest "type" was used by foresters in practically the same sesne that "association" is now used by many ecologists long before the latter term originated, and still continues in good usage.—EDITOR.]

Investigations by Bates[2] in the Central Rocky Mountains yield conclusions at variance with the above conception as regards moisture requirements. His experiments indicate that the species inhabiting dry sites, such as western yellow pine, utilize more moisture in the production of a unit of dry matter than do the species occupying relatively humid sites, *e.g.*, Douglas fir and Engelmann spruce.. These findings may strike the reader as being revolutionary, but a moment's reflection will show them to be in accord with actual conditions. In the San Francisco Mountains, the Engelmann spruce forests receive approximately 50 percent more precipitation than do the yellow pine forests. The average spruce stand, however, yields roughly 25,000 board feet of saw timber per acre in 100 years against about 8,000 board feet of yellow pine in 200 years. Thus the spruce appears to be about six times as economical in water consumption as is yellow pine. A large part but by no means all of this difference may be accounted for by the greater loss through direct evaporation in the yellow pine type.

Of greater importance than the moisture requirement as related to the production of dry matter is the moisture required for normal development. A species with high requirements per unit of material produced may, by reason of its slow growth, be able to maintain itself where the species of lower requirements in proportion to material produced can not exist. Moreover, we must also consider the capacity of a plant for obtaining water, as determined by its normal root spread. It is a matter of common observation that species occupying dry sites usually have a much greater root area than species occupying relatively moist sites. This relation is amply illustrated by western yellow pine and Engelmann spruce. To what extent root habit is a fixed character is a matter on which our knowledge is limited.[3] It may well be doubted, however, whether Engelmann spruce would under any conditions be able to attain the depth and spread of root exhibited by western yellow pine. If such be the case, it is conceivable that yellow pine on a dry site, even with its relatively high demands, might be able to more fully satisfy its needs for moisture than Englemann spruce with its lower requirements.

Looking at the matter in this light, the common conception regarding moisture requirements, namely, that the species of highest requirements occupy the most humid climatic zones, is probably correct. As regards temperature requirements, the usual assumption that the species occupying the warmest sites are there because they require high temperature for normal development, seems to be generally accepted, though it is conceivable that this may not necessarily be the case. Foresters must recognize that this field is still undeveloped and that exhaustive studies may be expected to yield a wealth of information. With this situation in view an investigation known as "The Study of Forest Types" has been undertaken by the Forest Service in various sections of the West. In brief, the object has been to correlate the occurrence of tree species with physical environment in different forest types or associations, and thus to determine what conditions are favorable and what unfavorable to each species. Such a study has been in progress at the Fort Valley Experiment Station in the San Francisco Mountains of Arizona during the past two years. The principles here developed are, according to the writer's observations, applicable to the entire Southwest, although it is recognized that they may be subject to more or less modification under conditions peculiar to certain localities. Although the study is still incomplete, sufficient progress has been made to warrant a preliminary presentation of results.

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[2] Bates, C. G., "Forest Types of the Central Rocky Mountains" (being published by the U. S. Weather Bureau).

[3] For interesting material on the root habit of certain forest trees see Pulling, N. E., "Root Habit and Plant Distribution in the Far North," Plant World, Vol. 21, No. 9, pp. 223–233, 1918.

Waterman, W. G., "Development of Root Systems under Dune Conditions," Bot. Gaz., Vol. 68, No. 1, pp. 22–53, 1918, finds some rather striking relations between root spread and the chemical composition of soils.

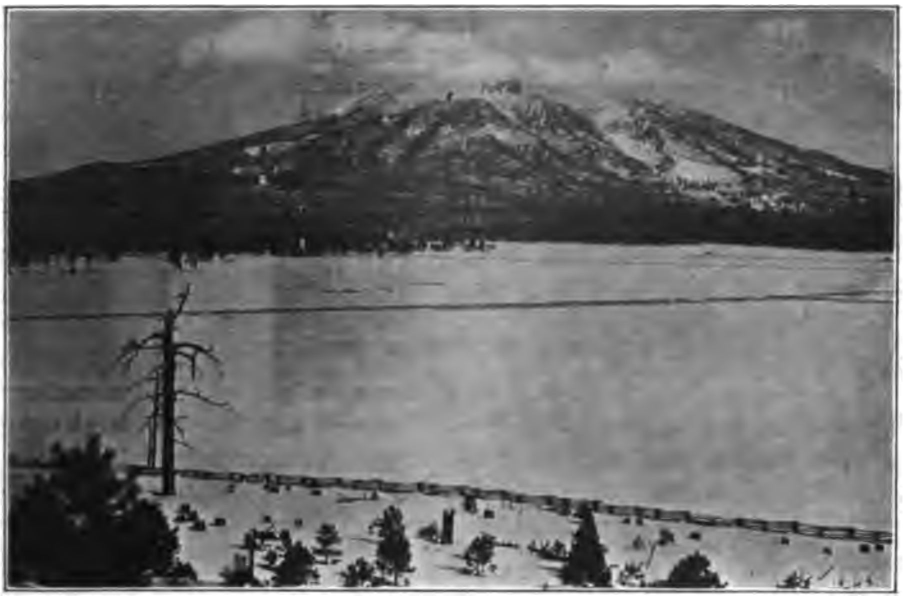

FIG. 1. The San Francisco Mountains with Fort Valley in the foreground. The numbers indicate the location of the meteorological stations as follows: 1, yellow pine; 2, Douglas fir; 3, limber pine; 4, Engelmann spruce; 5, timber line.

Before proceeding with the discussion, a brief statement of the general circumstances under which the study has been conducted is in order.

First, the writer desires to acknowledge the services of his associates at the Fort Valley Experiment Station. An understanding of the physical difficulties presented by this investigation may be gained when it is considered that for over two years weekly or semi-weekly trips have been made from the Experiment Station headquarters to timberline, involving a climb of over 4,000 feet. In the winter this climb is often hazardous and calls for great physical endurance.[4]

Due to various circumstances, the records at the high altitude stations have occasionally been broken. This applies particularly to the timberline station which has been inaccessible during considerable periods each winter. Whenever it has been necessary to use incomplete data in computing mean values here presented this fact has been indicated, and when the data are so meager as to be untrustworthy they have been omitted.

The meteorological data for Kingman, Williams, Flagstaff and Winslow are taken from U. S. Weather Bureau records. The records for Ash Fork were kept by Forest Ranger Frank J. Cox and those for Walnut Canyon by Mrs. W. H. Pierce. All other data have been obtained directly by the Experiment Station.

PHYSICAL CHARACTERISTICS OF THE FOREST TYPES

The climate of the Southwest, while determined primarily by its southern latitude and geographical location, is so strongly diversified by local topographic features that nothing but a most general description will apply to any extensive section. Areas below 4,000–5,000 feet elevation are characterized by extreme aridity and high summer temperatures, associated with desert vegetation. As the higher altitudes are reached there is a gradual increase in precipitation and decrease in temperature accompanied by added luxuriance in vegetation which culminates in magnificent spruce forests at 10,000 to 11,000 feet elevation. Latitude is distinctly subordinate to altitude in determining climatic variations within this region.

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[4] The primary instrument stations were established in the fall of 1916 by Forest Assistants Emanuel Fritz and Lenthal Wyman who maintained the records through the following winter and spring. During the summer and fall of 1917 observations were continued successively by Forest Assistants T. S. Hansen, C. E. Behre and S. S. Van Boskirk. From December, 1917, to July, 1918, the work was carried on by Forest Ranger Landis J. Arnold, and from July, 1918, to May, 1919, by Forest Ranger J. E. Kintner. During this entire period, the writer has maintained close supervision over the work, and at intervals, in the absence of assistance, has handled it in person. Since June, 1918, the formidable task of compiling the data has been greatly facilitated by the efficient service of Forest Clerk Miss Maude E. Wilson, whose work has made it possible to keep the compilations well up to date. Mr. J. O. Veatch, of the Bureau of Soils, has rendered valuable assistance in the classification of soils. His work, which promises to yield rich returns, is just beginning as this article is being completed. Grateful acknowledgment is also made to Mr. Raphael Zon, Chief of Forest Investigations of the Forest Service, for his many helpful suggestions and his unfailing encouragement throughout this investigation. The frequent changes in personnel indicated by the numerous assignments to this project are due to war conditions. Obviously the work has suffered from these changes.

The territory covered by this study comprises an altitudinal range of 6,400 feet, extending from 5,100 to 11,500 feet elevation, within a horizontal distance of about 55 miles, and is generally typical of forest conditions on the Colorado Plateau. Foresters recognize five main forest types or plant associations which are distinguished by the predominant tree species. Their approximate altitudinal arrangement is as follows:

Forest Type	Altitude	Predominating Species
Pinon-juniper	5,000– 6,700	*Juniperus monosperma* (Engelm.) Sarg. *Juniperus utahensis* (Engelm.) Lemm. *Pinus edulis* Engelm.
Yellow pine	6,700– 8,300	*Pinus ponderosa scopulorum* Engelm.
Douglas fir	8,300– 9,500	*Pseudotsuga taxifolia* (Lam.) Britton *Pinus flexilis* James *Abies concolor* (Gord.) Parry *Populus tremuloides* Michx.
Engelmann spruce......	9,500–11,500	*Picea engelmanni* Engelm. *Abies arizonica* Merriam *Pinus aristata* Engelm. *Populus tremuloides* Michx.
Alpine	Above 11,500	Trailing forms of *Picea engelmanni* and *Pinus aristata*

Anyone familiar with mountain conditions will understand that the above limits are only approximate. On the average they will run about 500 feet higher on south exposures and about 500 feet lower on north exposures. Moreover, there is more or less interlapping, thus forming a transition zone between types.

Using the Fort Valley Experiment Station (altitude 7,300 ft.) in the yellow pine type as a base, stations for the study of climate, soil, and vegetation were established in each forest type. In addition, a number of temporary substations have been established for the purpose of determining local variations within the type. Climatic studies include air temperature, precipitation, evaporation and wind movement. The soil studies include temperature and moisture content at different depths, and physical and chemical analyses. Studies of vegetation involve a listing of native species and also the cultivation of plants both indigenous and exotic. Weekly or semi-weekly readings have been made continuously for two years, excepting at the base stations where daily readings have continued over nine years. At all the primary stations continuous records of air temperature, and at some of the stations soil temperature, have been secured by means of thermographs.

All of the primary stations are located in typical forests of the character they are designed to represent. It is recognized that this necessitates reckoning with the influence of the forest itself. This course was adopted, however, because what is wanted is a knowledge of the conditions under which the trees actually grow. By means of check stations it is possible to establish reducing factors for different conditions of cover, slope, exposure, etc.

Thermometers and anemometers have with few exceptions been exposed at a height of eight feet above the ground. It is especially desirable to measure the conditions to which young growth is subjected, and these conditions could be secured better by placing the instruments close to the ground. But this was considered impractical because the deep snows would cover them. Check readings are, however, being made in order to establish a relation between surface temperature and that at eight feet. Evaporation has been measured mainly from free water surfaces by means of tanks 15 inches in diameter. Porous cup evaporimeters have been used to some extent, but their continuous use is interfered with by the occurrence of frost during the growing season, particularly in the spring and fall when evaporation is of greatest importance. Living plants have also been employed to a limited extent. Soil temperatures have been measured both with standard soil thermometers and with ordinary thermometers suspended in a tube at the desired depth. For depths exceeding 1 foot an ordinary metal pipe closed at both ends is used. Originally these pipes were also used for shallower depths, but on account of the possible effect of conduction by the metal, they have been replaced by wooden tubes.

TEMPERATURE.—Comparisons of the various forest types with respect to temperature are given in Tables 1 to 8 and figures 1 to 3. The usual relation between altitude and temperature holds here in a general way. The altitudinal mean temperature gradient from Kingman at 3,300 feet to timber line on the San Francisco Mountains at 11,500 during 1917 and 1918 was 3.68° F. for each 1,000 feet. Observations on other mountains, according to Hahn,[5] have given the following gradients: Pikes Peak 3.46° F.; Sierra Nevadas (Colfax, Placer Co., California) 4.12°; free air gradient Blue Hill Observatory 2.5°. Shreve[6] finds a gradient of 4.11° in the Santa Catalina Mountains of southern Arizona. As shown in figure 2, the fall in temperature in the San Francisco Mountains is by no means constant for a given rise in elevation. Comparing all the stations, the least difference is found between the yellow pine and Douglas fir stations, representing an altitudinal difference of 1,600 feet. In many instances the relation between these two stations has shown an actual inversion, the highest temperatures being found at the highest altitude. The same condition was found by Shreve in the Santa Catalina

[5] Hann, J., "Handbuch der Klimatologie," p. 245.

[6] Shreve, Forrest, "The Vegetation of a Desert Mountain Range as Conditioned by Climatic Factors," Carnegie Inst. of Wash. Publ. 217, 1915.

Mountains between 2,000 and 4,000 feet. Analysis of the records shows that the irregularities in the temperature gradient are due mainly to irregularities in the minimum. The maximum shows a very uniform gradient.

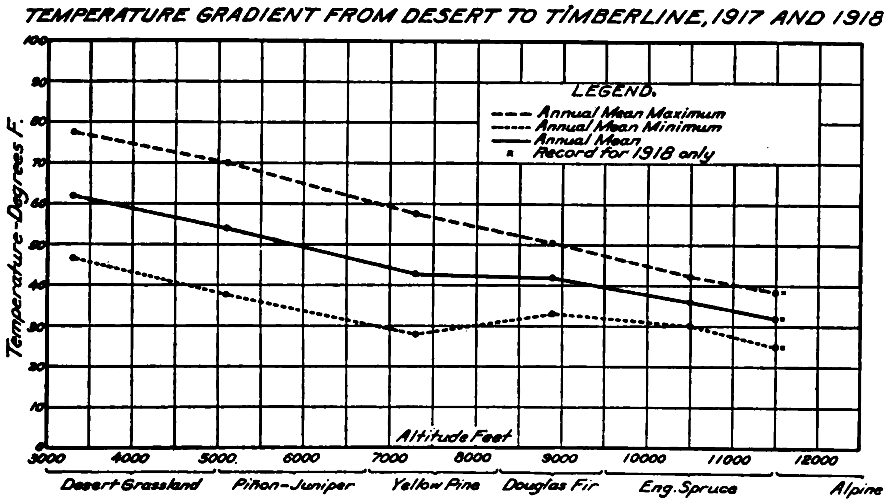

FIG. 2.

The erratic behavior of minimum temperatures in relation to altitude is one of the most striking things brought out in this study, although similar conditions have been found elsewhere. Extreme minimum temperatures are usually lower in the yellow pine type than at any of the higher stations, even

TABLE 1. *Temperature, annual and growing season. Means 1917 and 1918, degrees F.*

Forest type	Annual				June–September		
	Alt. Ft.	Mean	M. Max.	M. Min.	Mean	M. Max.	M. Min.
Desert-Grassland							
Kingman	3,300	62.1	77.5	46.6	79.9	95.3	64.4
Winslow	4,850	53.8	......	......	73.0	90.8	55.2
Pinon-Juniper							
Ash Fork	5,100	54.2	70.2	38.1	71.1	87.6	54.6
Cosnino[a]	6,500	......	......	......	65.6	82.4	48.8
Yellow Pine							
Williams	6,750	47.4	63.5	31.3	65.6	82.1	49.1
Walnut Canyon	6,700	......	......	......	64.8	82.3	47.4
Flagstaff	6,900	44.2	59.0	29.4	61.4	77.2	45.7
Fort Valley	7,300	42.5	57.6	27.4	59.5	75.3	43.8
Douglas Fir	8,900	41.7	50.5	33.0	56.9	67.1	46.6
Engelmann Spruce	10,500						
N. W. Slope, cover	......	36.0	42.1	29.9	51.4	58.2	44.5
S. W. Slope, open[ab]	......	37.5	45.0	30.0	52.0	61.2	42.8
Alpine[ab]	11,500	31.9	38.6	25.1	47.8	55.1	40.4

[a] 1918 record only.

[b] Interpolated in part.

TABLE 2. *Mean temperature by months, 1917 and 1918, degrees F.*

Forest type	Jan.	Feb.	Mch.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Desert-Grassland													
Kingman[a]	41.4	46.2	51.2	58.5	61.9	78.9	83.4	80.4	77.1	65.2	53.0	47.3	62.1
Winslow	28.4	38.8	44.0	51.1	58.3	73.3	76.9	73.8	67.7	56.7	42.8	33.3	53.8
Pinon-Juniper													
Ash Fork[b]	34.3	38.1	42.6	50.3	54.9	71.3	74.4	71.2	67.8	58.3	46.5	40.9	54.2
Yellow Pine													
Williams	27.0	33.3	37.3	43.1	48.8	64.8	67.8	64.0	61.0	49.8	38.9	33.5	47.4
Flagstaff	23.5	29.5	33.6	40.3	45.6	62.1	64.6	61.8	57.2	48.1	34.8	30.2	44.3
Fort Valley	23.1	27.5	30.4	37.7	42.5	59.9	62.3	60.3	55.8	47.1	34.1	29.5	42.5
Douglas Fir	24.6	27.7	30.7	37.3	41.7	60.1	58.1	56.3	53.2	46.7	34.5	30.8	41.8
Engelmann Spruce	20.8	21.5	23.5	29.6	34.6	52.9	52.6	52.4	47.8	41.4	29.4	26.1	36.0
Alpine[c]	15.7	17.2	23.1	26.2	30.8	51.6	48.1	46.8	44.7	35.4	23.5	19.3	31.8

[a] Incomplete for April, July, September and October, 1917. Interpolated for March, 1917.

[b] Incomplete for January, October and November, 1917.

[c] Records for 1918 only. Incomplete for February, March, November and December.

TABLE 3. *Mean maximum temperature by months, 1917 and 1918, degrees F.*

Forest Type	Jan.	Feb.	Mch.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Desert-Grassland													
Kingman[a]	54.3	60.9	67.8	76.3	78.2	98.0	98.3	94.6	90.6	82.4	67.5	61.6	77.5
Pinon-Juniper													
Ash Fork[b]	48.6	50.1	57.2	66.6	70.2	90.1	89.6	86.4	84.5	76.7	65.2	58.3	70.3
Yellow Pine													
Williams	40.7	45.7	51.5	59.0	63.4	84.8	83.9	81.2	78.6	68.8	55.7	49.1	63.5
Flagstaff	37.6	41.2	46.7	54.4	59.8	80.2	78.3	76.6	73.1	64.9	50.5	45.5	59.1
Fort Valley	37.4	40.0	44.3	51.8	57.2	78.0	76.6	75.1	71.7	64.0	49.6	45.5	57.6
Douglas Fir	30.1	34.6	39.0	46.3	52.4	72.1	67.5	66.3	62.8	56.1	42.0	37.3	50.5
Engelmann Spruce	25.9	26.2	29.9	36.6	42.6	61.1	59.4	58.7	53.8	46.6	34.6	30.3	42.1
Alpine[c]	21.6	24.0	29.0	34.1	38.9	59.5	54.9	53.8	52.2	41.2	30.0	23.5	38.5

[a] Incomplete for April, July, September, October, 1917. Interpolated for March, 1917.

[b] Incomplete for January, October, November, 1917.

[c] Records for 1918 only. Incomplete for February, March, November and December.

timber line (Table 7). Above and below the yellow pine type the trend is normal. The low temperatures in the yellow pine are due to air drainage; cold air currents descend from the high mountain slopes and spread out over the mesas and valleys below. Previous investigations in this region[7] have shown that in valleys, particularly where devoid of forest cover, minimum temperatures are commonly 10 to 15 degree lower than on nearby timbered uplands. The descent from the yellow pine to the pinon-juniper type is accompanied by a gradual rise in minima and a very rapid rise in maxima.

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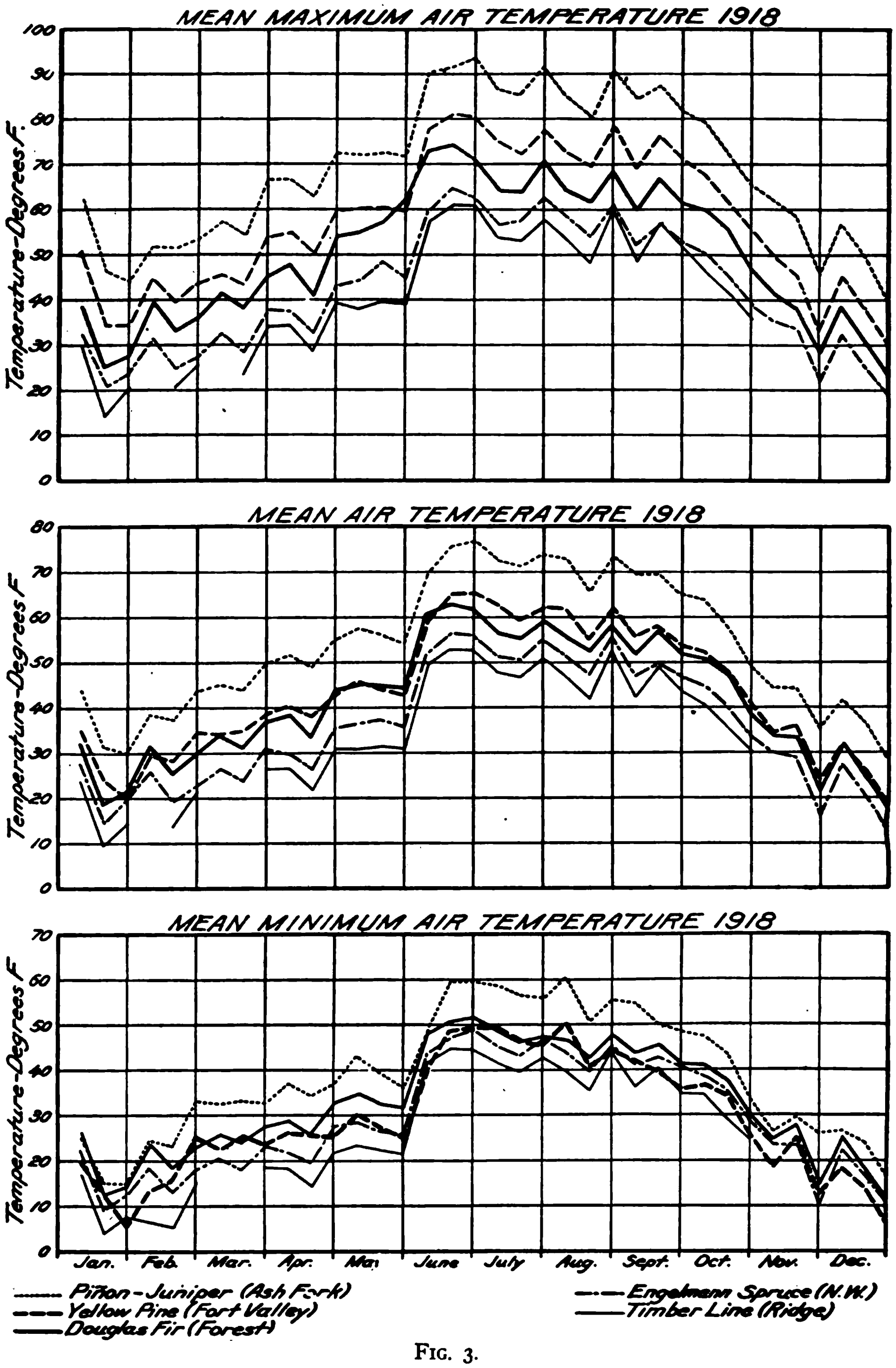
[7] Pearson, G. A., "A Meteorological Study of Parks and Timbered Areas in the Western Yellow Pine Forests of Arizona and New Mexico," Monthly Weather Review, Vol. 41, pp. 1615–29, 1914.


MEAN MAXIMUM AIR TEMPERATURE 1918
Temperature-Degrees F.
100
90
80
70
60
50
40
30
20
10
0
MEAN AIR TEMPERATURE 1918
Temperature-Degrees F
80
70
60
50
40
30
20
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0
MEAN MINIMUM AIR TEMPERATURE 1918
Temperature-Degrees F
70
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50
40
30
20
10
0
Jan.
Feb.
Mar.
Apr.
May
June
July
Aug.
Sept.
Oct.
Nov.
Dec.
Piñon-Juniper (Ash Fork)
Yellow Pine (Fort Valley)
Douglas Fir (Forest)
Engelmann Spruce (N.W.)
Timber Line (Ridge)

FIG. 3.

TABLE 4. *Mean minimum temperature by months, 1917 and 1918, degrees F.*

Forest type	Jan.	Feb.	Mch.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Desert-Grassland													
Kingman[a]	28.4	31.5	34.7	40.7	45.7	59.9	68.6	66.2	63.7	48.1	38.4	33.0	46.6
Pinon-Juniper													
Ash Fork[b]	19.9	26.0	28.0	33.9	39.5	52.5	59.1	56.0	51.0	39.9	27.8	23.4	38.1
Yellow Pine													
Williams	13.2	20.8	23.0	27.2	34.2	44.7	51.7	46.7	43.4	30.8	22.0	17.8	31.3
Flagstaff	9.4	17.8	20.5	26.2	31.3	43.9	50.8	47.0	41.2	31.3	19.1	14.9	29.5
Fort Valley	8.8	14.9	16.4	23.6	27.7	41.7	47.9	45.5	39.9	30.2	18.5	13.5	27.4
Douglas Fir	19.0	20.8	22.3	28.3	31.0	48.1	48.7	46.3	43.6	37.2	27.0	24.2	33.0
Engelmann Spruce	15.7	16.8	17.1	22.6	26.5	44.6	45.8	46.0	41.7	36.2	24.2	21.8	29.9
Alpine[c]	9.7	10.3	17.3	18.3	22.7	43.6	41.3	39.7	37.1	29.6	17.0	15.0	25.1

[a] Incomplete for April, July, September, October, 1917. Interpolated for March, 1917.

[b] Incomplete for January, October, November, 1917.

[c] Records for 1918 only. Incomplete for February, March, November and December.

TABLE 5. *Mean daily range of temperature by months, 1917 and 1918, degrees F.*

Forest type.	Jan.	Feb.	Mch.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Desert-Grassland													
Kingman[a]	25.9	29.4	33.1	35.6	32.5	38.1	29.7	28.4	26.9	34.3	29.1	28.6	30.9
Pinon-Juniper													
Ash Fork[b]	28.7	24.1	29.2	32.7	30.7	37.6	30.5	30.4	33.5	36.8	37.4	34.9	32.2
Yellow Pine													
Williams	27.5	24.9	28.5	31.8	29.2	40.1	32.2	34.5	35.2	38.0	33.7	31.3	32.2
Flagstaff	28.2	23.4	26.2	28.2	28.5	36.3	27.5	29.6	31.9	33.6	31.4	30.6	29.6
Fort Valley	28.6	25.1	27.9	28.2	29.5	36.3	28.7	29.6	31.8	33.8	31.1	32.0	30.2
Douglas Fir	11.1	13.8	16.7	18.0	21.4	24.0	18.8	20.0	19.2	18.9	15.0	13.1	17.5
Engelmann Spruce	10.2	9.4	12.8	14.0	16.1	16.5	13.6	12.7	12.1	10.4	10.4	8.5	12.2
Alpine[c]	11.9	13.7	11.7	15.8	16.2	15.9	13.6	14.1	15.1	11.6	13.0	8.5	13.4

[a] Incomplete for April, July, September, October, 1917. Interpolated for March, 1917.

[b] Incomplete for January, October, November, 1917.

[c] Records for 1918 only. Incomplete for February, March, November and December.

TABLE 6. *Frostless period*

Forest type	Alt.	First and last killing frost				Length of frostless period (days)	
		1917		1918			
		Spring	Fall	Spring	Fall	1917	1918
Desert-Grassland							
Kingman	....	4/18	11/30	......	......	226	......
Pinon-Juniper							
West (Ash Fork)	5,100	6/1	10/19	5/30	10/18	140	140
East (Cosnino)	6,500	......	......	5/31	9/24	......	116
Yellow Pine							
Walnut Canyon	6,700	6/6	9/27	5/31	9/24	113	116
Flagstaff	6,900	6/6	9/27	5/31	9/24	113	116
Fort Valley	7,300	6/12	9/25	5/31	9/17	105	109
Douglas Fir	8,900	6/2	10/18	5/31	10/18	137	140
Engelmann Spruce	10,500	6/5	9/24	5/31	9/25	111	117
Alpine	11,500	6/5	9/23	6/1	9/23	110	114

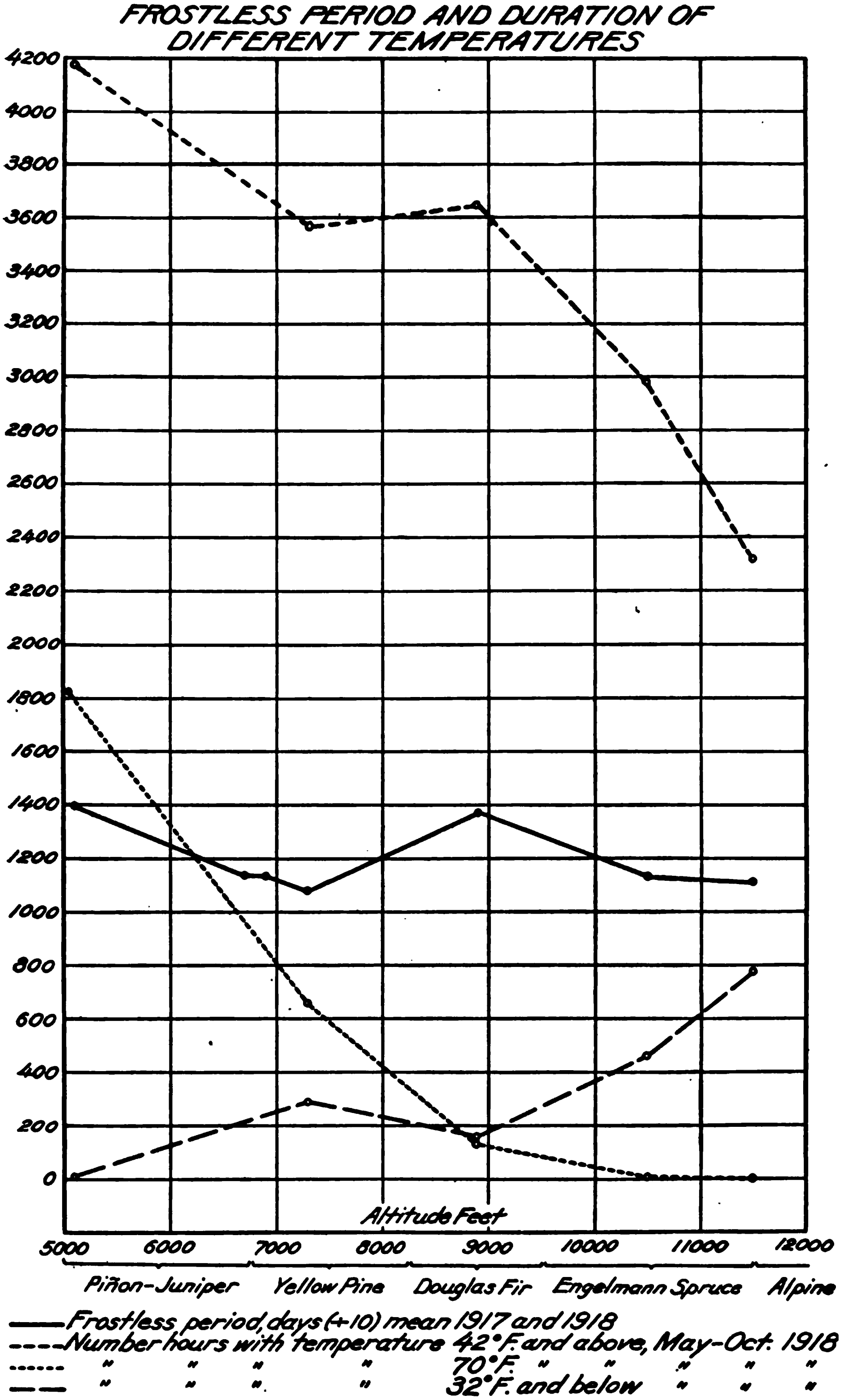
FROSTLESS PERIOD AND DURATION OF DIFFERENT TEMPERATURES
4200
4000
3800
3600
3400
3200
3000
2800
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
Altitude Feet
5000
6000
7000
8000
9000
10000
11000
12000
Piñon-Juniper
Yellow Pine
Douglas Fir
Engelmann Spruce
Alpine
——Frostless period, days (×10) mean 1917 and 1918
----Number hours with temperature 42°F. and above, May-Oct. 1918
...... " " " " 70°F. " " " " "
—— " " " " 32°F. and below " " "

Fig. 4.

The length of the frostless period as determined by the occurrence of temperature below 32° F. is shown in Table 6 and figure 4. It is noteworthy that the shortest frostless season occurs at stations in the yellow pine type. Even in the alpine type the first killing frost in the fall of 1918 occurred a week later than at the Fort Valley Station in the yellow pine type. The Douglas fir type has the longest frostless period of the high mountain types; in 1918 is was as long as at Ash Fork, nearly 4,000 feet lower.

TABLE 7. *Lowest temperatures by months, 1918, degrees F.*

Forest type	Jan.	Feb.	Mch.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Desert-Grassland												
Kingman.....	21.0	21.0	28.0	27.0	35.0	49.0	53.0	50.0	51.0	38.0	24.0	11.0
Winslow......	− 9.0	12.0	18.0	17.0	30.0	40.0	52.0	44.0	38.0	23.0	14.0	− 1.0
Pinon-Juniper												
Ash Fork.....	0	14.0	23.0	24.0	31.0	41.0	50.0	46.0	37.0	27.0	11.0	9.0
Yellow Pine												
Williams.....	− 3.0	2.0	12.0	18.0	21.0	28.0	39.0	35.0	26.0	18.0	0	− 7.0
Flagstaff.....	−13.0	3.0	11.0	16.0	18.0	32.0	42.0	36.0	25.0	16.0	− 4.0	−10.0
Fort Valley...	− 6.0	−13.0	6.0	15.0	12.0	33.0	40.0	34.0	25.0	15.0	− 4.0	−10.0
Douglas Fir.....	− 2.0	4.0	14.0	18.0	23.0	39.0	43.0	41.0	33.0	20.0	8.0	− 2.0
Engelmann												
Spruce.......	− 6.0	2.0	9.0	13.0	19.0	35.0	39.0	38.0	32.0	17.0	2.0	− 6.0
Alpine.........	− 3.0	− 2.0	9.0	5.0	13.0	30.0	34.0	33.0	29.0	10.0	2.0	......

Invariably the highest temperatures occur in the lowest altitudes (Table 3). In the spruce and alpine types temperatures above 70° F. are exceedingly rare, but in the yellow pine and pinon-juniper they are common from May to September. An idea of the relative duration of high temperature is obtained by comparing the stations with respect to the number of hours of temperature above 70° F. (table 8). For all excepting the pinon-juniper stations, the May–October total is also the annual total.

The daily range is greatest in the lower altitudes. In the pinon-juniper and yellow pine types we commonly find a daily range of 40 to 50 degrees, while in the spruce and alpine types it is rarely more than 20 (Table 5).[8]

The salient facts in regard to air temperature may be summarized as follows:

Mean temperature decreases as the altitude increases, except for local inversions in the gradient which occur rather frequently between the yellow pine and Douglas fir types. Departures from the general law are due

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[8] [This is the reverse of the conditions found in the Alps by Bonnier ("Le Monde végétal," E. F. Flammarion, Paris, 1914, p. 336), and indicated by brief records on Mt. Marcy, New York ("Plants and Animals of Mount Marcy, New York, Part I," Ecology, Vol. 1, No. 2, 1920). The reason is probably the dryness of the lower elevation in Arizona. The increase of moisture with altitude in Arizona would tend to counterbalance the decreased atmosphere and increased insolation, and thereby diminish the diurnal range of temperature. In a pluvial climate such as that of the Alps and eastern United States moisture does not increase so markedly with altitude.—EDITOR.]

TABLE 8. *Duration of different temperatures, 1918. Number of hours*

Forest type	32° F. or below		42° F. or above	70° F. or above	
	May–Oct.	June–Sept.	May–Oct.	June–Sept.	Annual
Pinon-Juniper Ash Fork	13 plus	0	4,177	1,489	1,872 plus
Yellow Pine Fort Valley	287	21	3,565	633	657
Douglas Fir	158	0	3,650	134	134
Engelmann Spruce	461	0	2,977	4	4
Alpine	779	24	2,324	1	1

to low minimum temperatures in the yellow pine type resulting from the descent of cold air currents from the upper mountain slopes. The lowest absolute minima and the shortest frostless period usually occur in the yellow pine type, followed closely by the alpine type. The highest temperatures and greatest duration of high temperature are found in the lowest altitudes. Maximum temperatures decrease uniformly from the lowest to the highest altitudes. The greatest daily range occurs in the lower types; in the spruce and alpine types, temperatures are very constant.[9]

PRECIPITATION.—Annual precipitation increases rapidly with altitudes up to the Douglas fir types (Table 9 and fig. 5). From there on to about 10,500 feet it remains nearly stationary, but beyond this point there appears to be a still further substantial increase. Considerable variability is exhibited in the relation between the upper stations. Thus in 1917, the Engelmann spruce station showed a slight excess over the Douglas fir station, while in 1918 the relation was reversed. Several years will be required to give a reliable comparison. As a rule records in other regions have shown a slight decrease from the intermediate to the highest elevations. The annual distribution is about the same for the various types. At the Fort Valley Experiment Station, where records have been maintained for nine years, the distribution is roughly as follows: winter (December–March), 40 percent; spring (April–May) 10 percent; summer (June–August) 30 percent; autumn (September–November) 20 percent.

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[9] [It would have been interesting if summations of temperature according to Merriam's plan or Lehenbauer's physiological method had been added. Sampson in his "Climate and Plant Growth in Certain Vegetative Associations," U. S. Dept. Agr. Bul. 700, 1918, states that such summations "have shown much promise in correlating air temperature with physiological plant activities." In a study of the factors causing timber line on mountains data was secured which, though insufficient for final conclusions, suggested that effective temperature may be the leading factor in causing timber line (see "Plants and Animals of Mount Marcy, Part I" p. 92; Ecology Vol. I, No. 2, 1920). It is interesting that in Pearson's table 8 giving the duration of different temperatures, the alpine had 653 hours, or 23 percent less, above 42° F. than the Engelmann spruce, and that this is the largest percentage decrease between any of the types. It is possible that this relationship would have been even more striking in a summation of effective temperature.—EDITOR.]

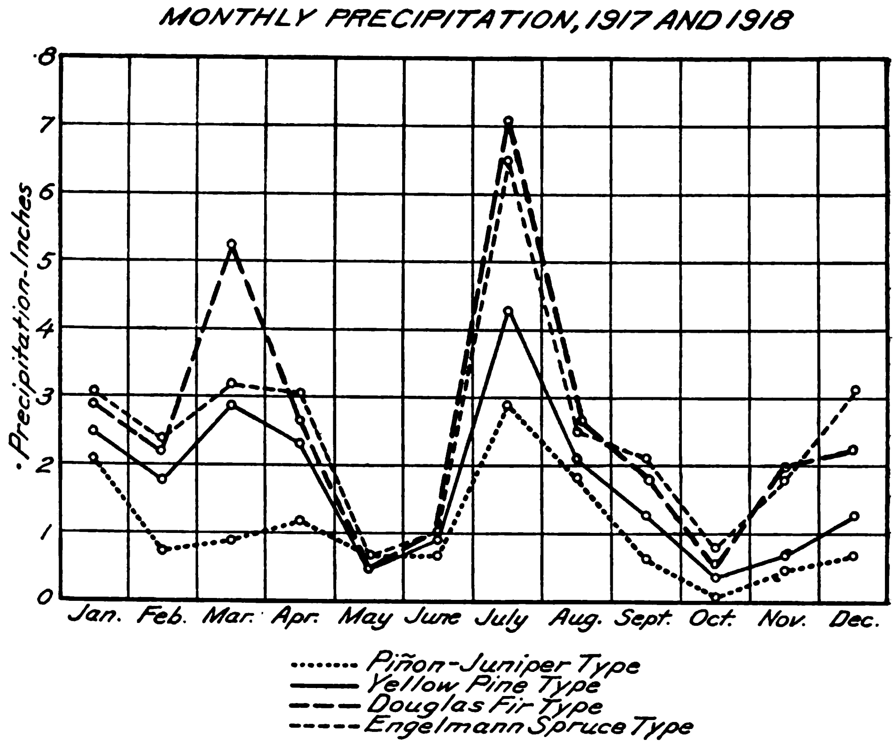

FIG. 5.

TABLE 9. *Precipitation*

	Alt. Ft.	Annual (inches)		June to September (inches)	
		1917	1918	1917	1918
Desert-Grassland					
Kingman	3,300	9.67	13.00	2.25	3.70
Winslow	4,850	7.38	....	4.93	....
Pinon-Juniper					
Ash Fork	5,100	13.99	12.36	7.05	5.21
Cosnino	6,500	....	....	4.91	8.40
Yellow Pine					
Williams	6,750	26.06	32.50	7.34	9.21
Walnut Canyon	6,700	....	....	6.65	7.45
Flagstaff	6,900	18.82	21.29	8.82	10.06
Fort Valley	7,300	17.81	24.27	7.43	9.89
Douglas Fir	8,900	23.60*	37.11*	12.21	12.95
Engelmann Spruce	10,500	....	....	....	....
N. W. Slope, cover	....	....	....	....	8.76
S. W. Slope, open	....	25.49*	35.16*	11.09	12.84
Alpine	11,500	....	40.23*	....	15.35

* Probable error of 1 to 2 inches due to inaccuracies in snow measurements.

Depth and duration of snow increase with altitude throughout the entire range. In the pinon-juniper type, snowfall is light and rarely stays on the ground more than a week at a time. In the yellow pine type it accumulates through the winter to a depth to 2 to 4 feet, but usually is all gone by April 1. In the Douglas fir type it becomes 3 to 4 feet deep and persists until about May 1. In the Engelmann spruce type the depth commonly reaches 6 feet and it stays on until the middle of June. In the alpine type the depth is uneven on account of drifting, the average being about 6 feet; it persists until the middle of June and in sheltered spots until the middle of July.

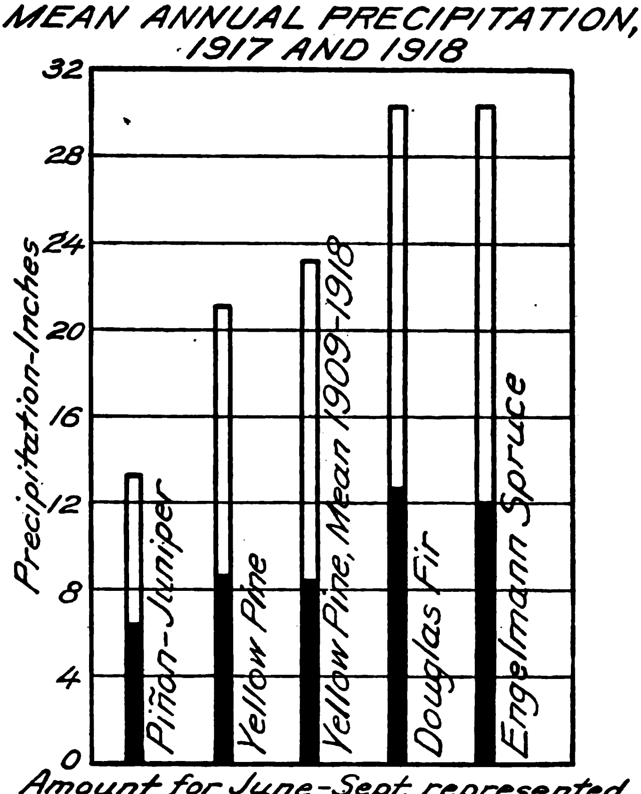

Fig. 6.

Throughout the range of forest types there are two periods of rather heavy precipitation separated by pronounced dry periods. The heavy snows leave the soil saturated with moisture which constitutes practically the entire supply until the advent of the summer rains in July. Intense drought usually prevails below the Douglas fir type through May, June, and the first half of July. During this period all but the deep rooted plants dry up, many stock watering places go dry, and the danger from forest fires is great. In the types above the yellow pine, although precipitation in April, May and June is light, the slowly melting snow keeps the soil moist. In the Douglas fir type there may be signs of drought in the latter part of June, but in the Engelmann spruce and alpine types the soil is usually moist right up to the beginning of the summer rains. The driest period in the Douglas fir and Engelmann spruce forests is usually in October and November.

WIND AND EVAPORATION.—Wind movement near the ground is determined mainly by the density of forest cover. The highest records are obtained in the alpine type, due mainly to the absence of forest cover. The lowest movement is recorded in the Engelmann spruce type where, on account of the dense forest, wind is scarcely discernible except at the tree tops. High velocities are the rule in the pinon-juniper type, owing to the fact that the trees are low and more or less scattering. In the yellow pine type high winds are experienced on clear-cut lands and other areas devoid of forest, but within stands of virgin timber wind movement is relatively light. The Douglas fir type is mostly free from high winds because areas on which the coniferous forest has been destroyed have grown up to aspen. Records for September, 1918, are given in Table 10.

TABLE 10. *Evaporation and wind*

Forest types	Evaporation from water surface, total inches		Wind movement, total miles	Ratio of evaporation to precipitation
	June to September		June to September	June to September
	1917	1918	1918	1918
Pinon-Juniper				
Ash Fork	....	41.95	.....	8.06
Yellow Pine				
Walnut Canyon	....	27.12	.....	3.66
Fort Valley	22.28	18.54	6,661	1.87
Douglas Fir	18.96	15.40	.....	1.19
Limber and Bristlecone Pine*	....	....	19,939	....
Engelmann Spruce*				
N. W. Slope, Dense cover	....	6.30	4,930	0.72
S. W. Slope, Opening	....	16.58	.....	1.29
Alpine*	....	19.34	23,494	1.26

* Interpolated June 1 to 13.

Evaporation is controlled mainly by temperature, relative humidity and wind. At some stations these factors combine so as to create high evaporation; at others the opposite effect is produced; while at still others one factor tends to neutralize the other. In the pinon-juniper we have high temperature, high wind movement and low relative humidity. The evaporation here is by far the highest recorded for any of the forest types (Table 10 and fig. 7). In the dense Engelmann spruce forest we have exactly reverse conditions, namely low temperature, practically no wind, and high relative humidity, with the result that this station has the lowest evaporation.

In the alpine type the low temperature favors low evaporation, but is counteracted by high wind movement, and as a result evaporation is relatively high.

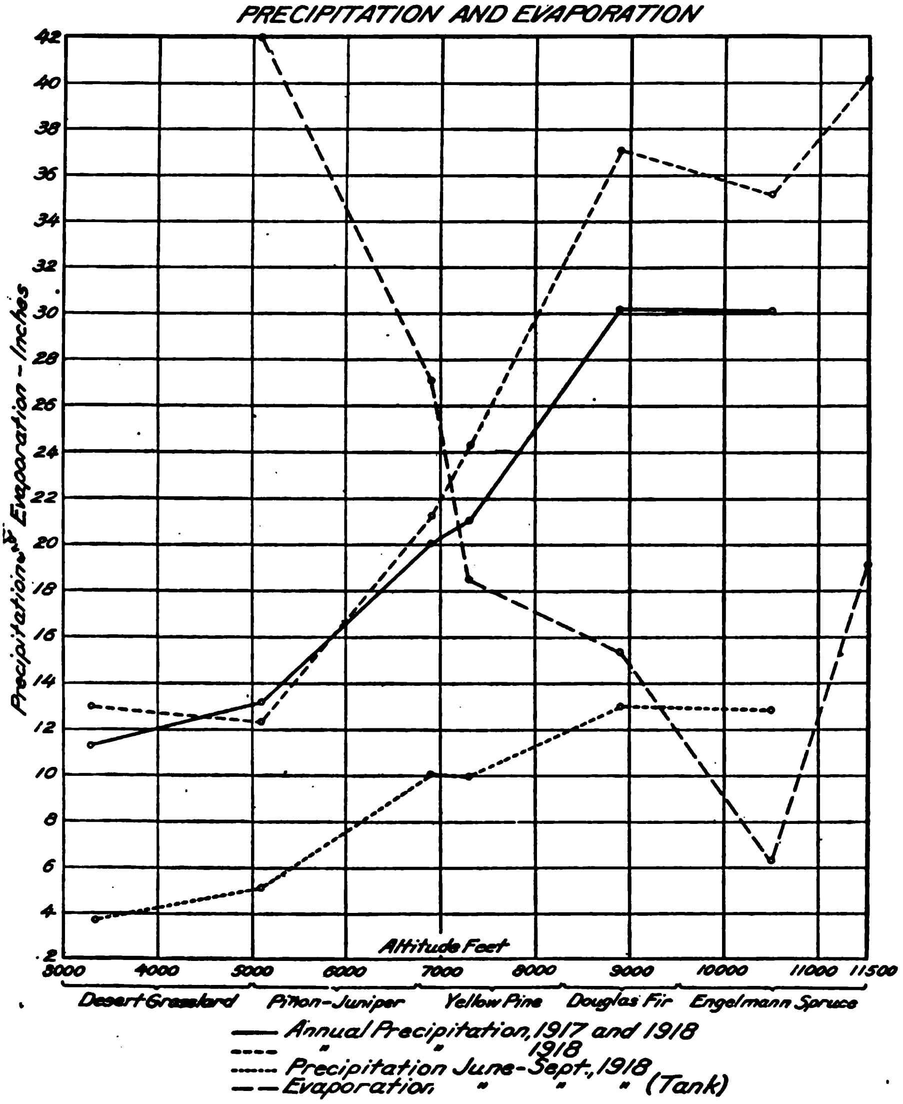

FIG. 7.

SOIL.—*Origin and General Character.*—On the basis of origin several general soil types occur in this locality, as determined by the rocks from which they are derived, mainly sandstones, limestones, basalt, dacites, andesites and ryolites.

In the pinon-juniper type we have soils derived from sandstones, limestones and basalt. The sandstones form a light sandy soil; the limestones usually form a fairly light surface soil, but a subsoil of clayey texture. The basaltic soils vary from a clay loam to a clay; and, unless mixed with a large proportion of gravel and rocks are somewhat impervious to roots and water.

Basaltic soils prevail over the greater portion of the yellow pine type. As in the pinon-juniper type they are of a compact, impervious structure unless, as is frequently the case, this condition is relieved by the admixture of gravel and stones. Sandstone and limestone soils similar to those described above occur locally in the lower half of the yellow pine type. Toward the upper limits of the type the soils are derived from a variety of volcanic rocks. These soils, since they occupy steep mountain slopes, are generally gravelly and stony throughout and are therefore very porous and easily penetrated by tree roots. They contain considerable humus in the surface layer, and grade into the succeeding belts of Douglas fir and Engelmann spruce.

Above the yellow pine type in the San Francisco Mountains the soil is almost entirely derived from volcanic rocks. In the Douglas fir and Engelmann spruce types the surface foot contains an appreciable amount of organic matter which, however, becomes less conspicuous as the alpine type is approached. In the Engelmann spruce type we find a forest mould from 2 to 4 inches thick. This is also present in the Douglas fir type, but here it is much thinner and less thoroughly decayed than in the Engelmann spruce type. In the pinon-juniper and yellow pine types, anything approaching a true forest mould occurs only close around the trees, and even here a large part of the material is undecayed.

Chemical analyses of the various soil types occurring in the San Francisco Mountains region reveal no difference of especial significance as related to vegetation. All are productive when supplied with sufficient moisture, and as far as can be determined the chemical composition is not an important factor in determining the distribution of species within the same climatic belt or vegetative zone. All the information at hand points to available moisture, as determined mainly by physical composition, as the dominant soil factor. As has been stated in previous publications[10] the admixture of sand, gravel and stone is believed to be vital in the adobe soils which without these constituents tend to become impermeable to both water and roots.

Soil Moisture.—Figure 8 shows the available soil moisture in the various forest types during the growing season of 1918. The plotted values represent the net percentages above the wilting point as determined by the centrifugal method of Briggs and Shantz[11] and computed according to their formula as modified by the Office of Dry Land Agriculture. The wilting point determinations are based upon too small a number of samples, and, moreover, the distribution of rainfall during the growing season of 1918 was considerably better than usual. For these reasons the data on soil moisture are not considered thoroughly satisfactory.

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[10] Pearson, G. A.,. "Studies of Yield and Reproduction of Western Yellow Pine in Arizona and New Mexico," Journal of Forestry, Vol. 16, No. 3, pp. 273–293, 1918 (especially p. 287); "The Relation between Spring Precipitation and Height Growth of Western Yellow Pine Saplings," idem, Vol. 16, No. 6, pp. 677–689, 1918 (especially p. 687).

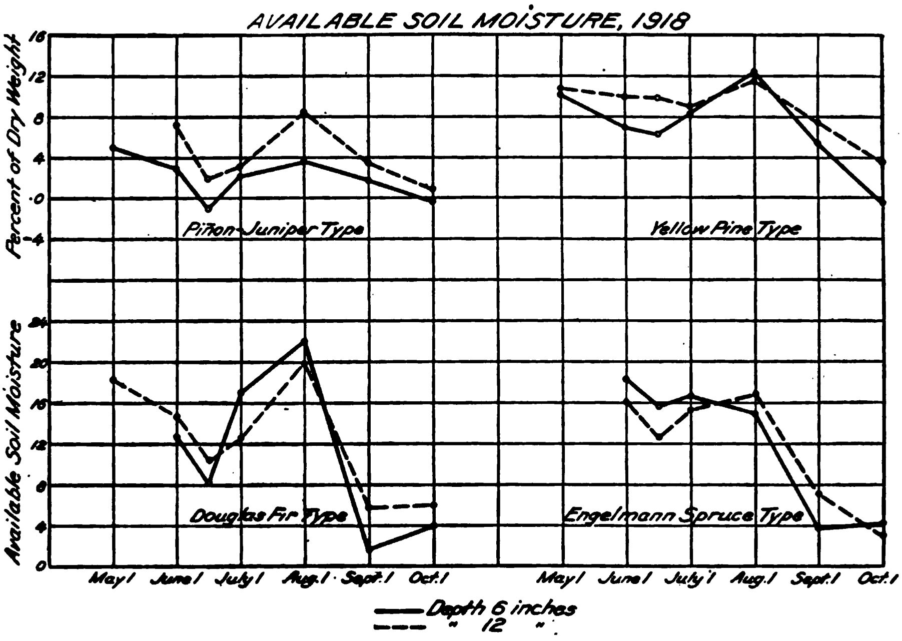

FIG. 8.

During the rainless period of May and June in 1918 moisture values approaching the wilting point at depths 6 inches or more below the surface were recorded only in the pinon-juniper type. In years of normal rainfall it is probable that equally low depressions occur in the yellow pine type. In the Douglas fir and Engelmann spruce types there is in normal years an abundance of soil moisture throughout this period, due to the deferred melting of snow which in the spruce forest persists into the month of June. It is the stored moisture resulting from the winter's snows which enables plants to live at all through May and June in the yellow pine and pinon-juniper types. In 1918 the early advent of the summer rains restored the rapidly declining moisture content in time to prevent its sinking to the low level which is reached in years when the summer rains begin from 2 to 4 weeks later. In 1918 the soil became driest about October 15, while in 1917 the lowest point was reached about December 31. Especially significant is the reduction in the lower strata even in the Engelmann spruce and Douglas fir types. Although the rainfall from June 15 to August 31, 1918, was close to 12 inches in both the Douglas fir and the Engelmann spruce types, the moisture content at a depth of 1 foot on October 1 was but slightly above the wilting coefficient. From this condition it is surmised that in all the forest types, regardless of rainfall, there is a tendency to exhaust the entire moisture supply during periods of active growth. Such a situation is conceivable when we consider the luxuriant vegetation in the types of heavy rainfall. If the results of this year's investigations are supported by measurements in 1919, it may become established that the most critical drought period for reproduction of all species is not in the fore-summer but in the fall. The data already at hand prove this to be the case for Douglas fir and Engelmann spruce but whether it is true of western yellow pine and pinon-juniper is less certain.

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[11] Briggs, L. J., and Shantz, H. L., "The Wilting Coefficient of Different Plants and its Indirect Determination," U. S. Dept. Agr. Bu. Pl. Ind. Bul. 230, 1912.

TABLE 11. *Soil temperature at 1 foot depth*

	Alt.	Aspect	Cover	Temperature degrees F.			
				Annual		May–Oct.	July–Oct.
				1917	1918	1918	1918
Pinon-Juniper							
Ash Fork (W)	5,100	Level	Open	....	....	71.2	72.6
Cosnino (E)	6,500	"	"	....	....	66.5	66.9
Yellow Pine							
Walnut Canyon	6,700	"	"	....	....	66.2	66.6
Fort Valley	7,300	....	......	....	....	......	....
Open	....	"	"	....	49.6	62.5	63.2
Partial Shade	....	"	Partial shade	....	45.7	56.2	57.6
Heavy Shade	....	"	Heavy shade	43.1	43.7	53.1	54.5
Douglas Fir	8,900	....	......	....	....	......	....
Last Y. Pine	8,900	South	Open	....	....	......	55.7
Forest	....	N.W.	Partial shade	39.6	40.8	48.8	49.6
Limber-Bristlecone	10,000	S.W.	Open	....	....	54.2*	54.2
Engelmann Spruce							
Forest	10,500	N.W.	Dense shade	34.9	35.2	40.8	43.4
Opening	....	S.W.	Open	....	....	47.0*	49.1
Alpine	11,500	W.	"	....	....	......	45.5

* Interpolated in part.

Soil Temperature.—Like mean air temperature, soil temperature (Table 11) falls with rising altitude. It furnishes a fairly good index to available heat energy. The bare soil is a good heat absorber, and at a depth of one foot or more it loses heat slowly. During the snowless period, soil temperatures taken in the open down to 6 inches in depth are usually several degrees higher than the mean or even the maximum air temperatures. During the period when the ground is continuously covered with snow, the soil temperature remains constantly at or a few degrees below 32° F. at all stations and at all depths down to 2 feet.

Experience has shown the selection of the site for soil thermometers to be exceedingly important. Exposure to the sun is the greatest factor. The difference in soil temperature between a north and a south exposure is much greater than the corresponding air temperature difference. The degree of shade as determined by crown cover is of tremendous importance. As shown by the records for "Open" and "Heavy Shade" at Fort Valley, in the yellow pine type (Table 11), the temperature at one foot is 6 to 9 degree F. lower in the shade of a group of trees than in an adjoining opening less than 100 feet away.

The diurnal fluctuation for depths of one foot is usually not more than 2 or 3 degrees F. In a moderately dense forest it is less than 1 degree. At the surface in the open it is much higher than the diurnal range of air temperature.

Since the soil temperatures at the mountain stations are based mainly upon weekly readings, except at the 6-inch depths for which thermographs are provided, many readers may question the reliability of the data presented in Table 11. Check readings at various times have shown that the error from this source is less than might be expected. The table below gives a comparison of means obtained by weekly and daily readings at the yellow pine station during the months of May and June, 1919. The differences at this season are as great as would be obtained at any other time of the year, and greatly exceed those of the winter and midsummer months.

Mean Soil Temperature (°F.)

	Heavy cover		Opening	
	Weekly readings	Daily readings	Weekly readings	Daily readings
May				
1st decade	43.1	43.5	49.1	49.8
2d decade	45.5	46.4	57.6	59.4
3d decade	49.7	48.7	58.5	57.3
Month	46.1	46.2	55.1	55.5
June				
1st decade	49.1	48.8	57.4	56.9
2d decade	52.7	53.1	66.7	66.0
3d decade	58.8	58.8	70.9	70.2
Month	53.5	53.6	65.0	64.4

The comparison shows a maximum error of 1.8° F. for a single decade in the open, and 1° under the cover of a group of trees. The maximum errors in the monthly means are 0.6° in the open and 0.1° under cover. The errors at the mountain stations would be less than those here indicated, because of generally lower temperature extremes, and in some instances because of denser forest cover. During periods when the ground is covered with snow, the error due to infrequency of readings is negligible.

(*To be concluded*)

SOIL ACIDITY AND A FIELD METHOD FOR ITS MEASUREMENT[1]

EDGAR T. WHERRY

Washington, D. C.

In a note on " Plant Distribution around Salt Marshes in Relation to Soil Acidity,"[2] the writer stated that many conclusions as to the relation between the distribution of plants and the reaction (acidity or alkalinity) of soils have been based on " misleading methods or unsound views as to the nature of soil acidity." It seems desirable that some evidence in support of this claim should be placed on record. The questions which have been most frequently asked the writer concerning the cause of soil acidity, the methods by which it can be measured, etc., will be answered as fully as possible from the standpoint of modern physical chemistry.[3]

WHAT IS THE CAUSE OF SOIL ACIDITY?

Soil acidity has been discussed by numerous workers, but considerable confusion as to its nature appears still to exist. To quote from a recent paper:[4] " Investigators have looked to the following substances and phenomena for the explanation of soil acidity: the presence of mineral acids, the presence of organic acids, free hydrogen ions, colloidal material, absorption and adsorption, and the presence of specific compounds." The writer of the foregoing added as his own view "hydrolytic mass action phenomena." Only one of the " substances and phenomena " of this list can be regarded as a direct " explanation of soil acidity," namely, the *presence of hydrogen-ion.*

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[1] [The influence of soil acidity on plant distribution has been amply demonstrated (Coville, U. S. Dep't. Agr. B. P. I., Bull. 193, 1910; Truog, Soil Science, 5: 169, 1918; 7: 469, 1919; Gillespie and Lewis, Soil Science, 4: 313, 1917; and many others). Its influence upon the animals living in the soil remains to be studied, but probably will prove no less important. Dr. Wherry discusses in simple terms the principles of physical chemistry which bear upon soil acidity, but usually can be found only in the more technical and less easily understood works. For convenience, his field method of measuring soil acidity (already published in the Jour. Wash. Acad. Sci. 10: 217, 1920) is included, and his indicator chart is reproduced for the first time in actual colors.—EDITOR.]

[2] Ecology, Vol. I, No. 1, pp. 42–48, 1920.

[3] It is a pleasure to acknowledge the aid received in the preparation of this paper from colleagues, especially from Dr. E. Q. Adams of the Bureau of Chemistry.

[4] Noyes, H. A., Journ. Ind. Eng. Chem., 11: 1040. 1919.

WHAT IS HYDROGEN-ION?

According to the almost universally accepted electrolytic-dissociation or ionization theory, many chemical compounds, under certain conditions, exhibit dissociation into electrically charged portions, known as *ions*. These may consist of single atoms or of groups of atoms. Only ionization connected with the dissolving of substances in water need concern us here. Compounds differ widely in the extent to which they are dissociated or ionized in dilute aqueous solution. Among inorganic compounds—acids, bases, and salts—many are almost completely, others only partially, ionized. Of organic compounds a few, especially acids, are markedly, a considerable number slightly, and many not appreciably ionized.

Water itself dissociates into *hydrogen-ion,* made up of positively charged hydrogen atoms, and accordingly symbolized by H^+; and *hydroxyl-ion,* made up of negatively charged hydroxyl (hydrogen plus oxygen) groups, symbolized by $(OH)^-$. Acids yield hydrogen-ion and another ion consisting of the balance of their constituents; thus from nitric acid, HNO_3, arise H^+ and $(NO_3)^-$, the latter being termed nitrate-ion. Alkalies yield hydroxyl-ion and another consisting of the remainder of the compounds; in potassium hydroxide, KOH, the ions are $(OH)^-$ and potassium-ion, K^+.

The amount of hydrogen-ion present in a solution, expressed as gram-equivalents per liter, is often referred to as the *hydrogen-ion concentration.*

The water existing in soils, as a film around the solid soil particles, does not differ essentially from free water in the above respects. Substances can dissolve in it, undergo ionization, and give rise to a definite hydrogen-ion concentration of the soil.

WHY SHOULD HYDROGEN-ION BE CONSIDERED IN CONNECTION WITH ACIDITY?

Observation has shown that the properties of substances which lead to their classification as acids are directly connected with the presence of hydrogen-ion in their solutions. The characteristic sour taste—from which the term acid was of course originally derived—is in considerable part the taste of hydrogen-ion.[5] Reddening of blue litmus, the most widely known test for acidity, is produced by hydrogen-ion. And it is hydrogen-ion which takes part in most of the chemical changes into which acids enter.

The inhibiting effect of acids on the growth of many bacteria, and the favorable effect they show toward the growth of some molds and fungi, are hydrogen-ion phenomena. There is every reason to suppose that the action of acids on higher organisms, such as the flowering plants, is identical in origin. It is evident from these considerations that the hydrogen-ion concentration is a highly important feature of the solution of any acid substance.

[5] Harvey, R. B., Journ. Amer. Chem. Soc., 42: 712. 1920.

HOW DOES HYDROGEN-ION CONCENTRATION DIFFER FROM QUANTITY OF ACID?

The difference between these two factors in the case of two typical acids is here tabulated. The numerical values given are only approximate.

TABLE 1. *Difference between hydrogen-ion concentration and quantity of acid in normal solutions of two acids*

	Acid	
	Hydrochloric	Formic
Formula	HCl	$H(CHO_2)$
Molecular weight = equivalent weight = grams per liter in normal (molar) solution	36.5	46.0
Quantity of acidic hydrogen, grams per liter	1	1
Physico-chemical class	strong	moderately weak
Percent. to which ionized	75	1
Corresponding hydrogen-ion concentration, grams per liter	0.75	0.01
Specific acidity	7,500,000	100,000

Table 1 shows that although a normal (molar) solution of both acids contains the same quantity of acidic hydrogen, the strong acid yields 75 times as much hydrogen-ion as does the moderately weak one, and may be expected to have 75 times as much effect in the directions listed under the preceding heading.

The situation is analogous to that of two men, both possessing $100, but one having $25 in a savings bank and $75 in his pocket, the other having $99 and $1 in these respective places. The first man can purchase 75 times the amount of any commodity that the second can, even though the total quantity of money they own is the same. Purchasing power, in this illustration, corresponds exactly to hydrogen-ion concentration; for the amount of hydrogen which is ionized, not the total amount, determines most of the things an acid can do.

HOW MAY HYDROGEN-ION CONCENTRATION BE MOST SATISFACTORILY EXPRESSED?

The relations between the various methods of expressing hydrogen-ion concentration which have been proposed can best be indicated by a tabular arrangement. In Table 2 the way two values selected at random appear under all of them is brought out; and the reader may judge whether the one chosen for use in the present paper (the last one tabulated, specific acidity) is not the best from the point of view of clearness and convenience. The hydrogen-ion concentrations of the two solutions, in gram-equivalents per liter, are 0.0004 and 0.0000002 respectively, the former representing 2,000 times as much hydrogen-ion as the latter.

TABLE 2. *Comparison of methods of stating hydrogen-ion concentration*[6]

	Method	Solution 1	Solution 2
Concentration	Actual number	0.0004	0.0000002
	Power of 10 with a coefficient	0.4×10^{-3}	0.2×10^{-6}
	Power of 10	$10^{-3.4}$	$10^{-6.7}$
Potential due to $H^+(P_H)$		3.4	6.7
Chemical potential, X_H	exponent	3.6	0.3
	power of 10	$10^{3.6}$	$10^{0.3}$
Specific acidity (water as unit)		4000	2

TABLE 3. *Specific acidity and alkalinity equivalents of P_H values*

A. Integral values of P_H

P_H	X_H	Specific acidity	P_H	X_H	Specific alkalinity
0	7	10,000,000	7	0	1
1	6	1,000,000	8	−1	10
2	5	100,000	9	−2	100
3	4	10,000	10	−3	1,000
4	3	1,000	11	−4	10,000
5	2	100	12	−5	100,000
6	1	10	13	−6	1,000,000
7	0	1	14	−7	10,000,000

B. Decimals of P_H

P_H	X_H	Specific acidity	P_H	X_H	Specific alkalinity
6.0	1.0	10 (10.00)	7.0	0.0	1 (1.00)
6.1	0.9	8 (7.94)	7.1	−0.1	1.3 (1.26)
6.2	0.8	6 (6.31)	7.2	−0.2	1.5 (1.58)
6.3	0.7	5 (5.01)	7.3	−0.3	2 (2.00)
6.4	0.6	4 (3.98)	7.4	−0.4	2.5 (2.51)
6.5	0.5	3 (3.16)	7.5	−0.5	3 (3.16)
6.6	0.4	2.5 (2.51)	7.6	−0.6	4 (3.98)
6.7	0.3	2 (2.00)	7.7	−0.7	5 (5.01)
6.8	0.2	1.5 (1.58)	7.8	−0.8	6 (6.31)
6.9	0.1	1.3 (1.26)	7.9	−0.9	8 (7.94)
7.0	0.0	1 (1.00)	8.0	−1.0	10 (10.00)
(For each lower P_H unit, multiply the specific acidity by 10)			(For each higher P_H unit, multiply the specific alkalinity by 10)		

The method illustrated in the last line of Table 2 obviously shows with a minimum of calculation on the part of the reader that one of the solutions is

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[6] The last two methods have been explained by the writer, Journ. Wash. Acad. Sci., 9:305. 1919.

2,000 times as acid as the other; and it gives directly the information that the hydrogen-ion concentration is in the one case 4,000 times, in the other case twice, that of pure water.

As the P_H method is rather widely used in the statement of hydrogen-ion concentration, it seems desirable that another table be given showing the relations between P_H values and specific acidities (and alkalinities) over the range covered by dilute aqueous solutions.

WHAT SUBSTANCES MAY YIELD HYDROGEN-ION TO THE SOIL SOLUTION?

This question can also be most instructively answered by a tabular statement.

TABLE 4. *Soil constituents yielding hydrogen-ion*

1. *Directly* (*when treated with water alone*)

A. Inorganic.
  a. Strong, highly ionized acids, like hydrochloric, sulfuric, etc.
  b. Weak, slightly ionized acids, especially carbonic.
  c. Acid salts, like potassium acid sulfate, which may be moderately or slightly ionized (as acids).
  d. Salts of weak bases with strong acids, like aluminium chloride, ammonium sulfate, etc., which are slightly hydrolyzed and therefore yield a small amount of hydrogen-ion.
B. Organic.
  a. Strong, highly ionized acids, like oxalic.
  b. Weak, slightly ionized acids, like acetic.
  c. Acid salts, like potassium acid sulfate, which may be moderately or slightly ionized (as acids).
  d. Salts of weak bases with strong acids, like aluminium citrate, ammonium oxalate, etc., which are hydrolyzed as in *A. d.*
  e. Amino-acids, like aspartic (aminosuccinic) acid, which are internal salts in the sense that the acidity is neutralized by the amino group, and which may be moderately or slightly ionized.
  f. Humic acids, which if they exist at all are slightly ionized.

2. *Indirectly* (*when treated with solutions of salts*)

A. Inorganic, especially colloidal clay.
B. Organic, especially colloidal humus.

From the above tabulation it is evident that soil acidity is likely to be a rather complex phenomenon, and it is certainly misleading for an investigator to look to any single substance or type of substances as the source of the hydrogen-ion producing it in all cases. As it seems probable, however, that comparatively few of these possible sources of hydrogen-ion, and accordingly of acidity, coexist in appreciable amounts in any one soil, the evidence for the presence of the several types of acid substances may well be reviewed.

ARE INORGANIC ACIDS PRESENT IN NATURAL SOILS?

There appears to be no reason to doubt that strong, highly ionized, inorganic acids exist in appreciable quantities in some soils. Nitric acid may be produced by nitrifying bacteria, sulfuric acid by the oxidation of sulfur-bearing compounds, hydrochloric acid through the interaction of sea-water and soils in the vicinity of salt marshes. Certain muck soils have been observed by Plummer[7] to exhibit hydrogen-ion concentrations equivalent to specific acidities as high as 200,000, which are comparable with the values shown by hundredth normal solutions of these acids.

The weak, slightly ionized carbonic acid, H_2CO_3, is probably universally present in soils, where it arises from the decomposition of carbonaceous matter. It can yield a maximum specific acidity of over 500, although in the presence of bicarbonate ion, which is rarely absent from the soil solution, this value may be greatly lessened.

If strong dibasic acids such as sulfuric develop in soils, and attackable compounds of potassium or other univalent elements are present in amounts insufficient to neutralize the acid completely, then acid salts will be formed. Potassium acid sulfate, $HKSO_4$, is rather highly ionized in dilute solution, yielding some hydrogen-ion (as well as various other ions), so this is by no means an unlikely source of soil acidity in certain cases.

Salts of aluminium and of iron may readily be formed by the action of strong acids upon silicates containing these elements; and such salts, because of the weakness of the bases, will through hydrolysis yield more or less hydrogen-ion. Similar relations hold for salts of ammonia and its derivatives, produced by the decomposition of nitrogenous organic matter; the bases are weak, and the salts yield hydrogen-ion. Such salts of weak bases with strong acids are likely to be the source of a considerable portion of the acidity of certain soils.

ARE ORGANIC ACIDS PRESENT IN SOILS?

Cellulose and other constituents of plant tissues are continually becoming incorporated with the soil. These decompose under the influence of various microorganisms, and among the decomposition products organic acids are likely to be represented. These may include strong, highly ionized acids like oxalic; moderately ionized ones like lactic; and weak, slightly ionized ones like acetic. Acid salts of any of these acids which are polybasic may form, as with inorganic acids; and the stronger of the organic acids may unite with weak bases to form salts, the result in both cases being the liberation of hydrogen-ion. Amino-acids are likely to develop from the decomposition of nitrogenous plant constituents, and also yield their quota of hydrogen-ion.

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[7] Journ. Agr. Research, 12: 22. 1918.

Probably no subject connected with soil acidity has been so extensively discussed as the question whether humic acids and related substances exist or not. It is not the intention of the writer to take sides in this controversy, but the physical-chemical aspect of the question may be briefly stated. It appears to have been definitely established that humus contains one or more substances which yield hydrogen-ion to pure water, and are therefore to be classed as acidic. Whether these substances are (1) of definite composition, and have their acidic hydrogen present in stoichiometric proportions; or (2), indefinite in composition, colloidal in character, and containing variable amounts of adsorbed hydrogen-ion, appears to be the chief point in dispute. Such sound evidence as has been presented seems to the writer to favor the second view, but as the matter has not been entirely settled, it is best to leave in the table a place for humic acids as a partial cause of soil acidity.

WHAT IS A COLLOID?

The term *colloid,* which is used (as an adjective) in the preceding paragraph, as well as in the final subdivision of Table 4, can be defined in a variety of ways, depending upon the use to which the definition is to be put. For the purposes of the present study, a colloid is any substance of which the constituent particles are of such size and shape that adsorption phenomena are prominently exhibited. *Adsorption* means the sticking of atoms, ions, or molecules of one substance to the surfaces of the particles of another substance. Nothing would be gained by entering into a discussion as to whether this effect is physical or chemical in nature, for there is good reason to believe it to represent a combination of both. It is physical in that adhesion and electromagnetic forces play a part in joining the substances. It is chemical in the sense that there is a union between the atoms of the substances by means of valence bonds, although since only atoms lying at the surfaces of the particles of the adsorbing substance take part, stoichiometric relations are not recognizable. The degree to which adsorption occurs in any given case depends, then, on the size and shape of the particles concerned, as well as on their chemical nature.

Soils contain colloids of two kinds, inorganic and organic. The former includes finely divided quartz and other minerals, silica gel, and gel forms of various more or less definite aluminium silicates, by far the most frequent of which has the formula $Al_2O_3.2SiO_2$. These substances are usually collectively known as clay. The organic colloids, conveniently grouped together under the term humus, comprise various complex compounds of carbon, hydrogen, and oxygen, arising from the partial distintegration of cellulose.

WHAT IS THE SIGNIFICANCE OF SUBSTANCES YIELDING HYDROGEN-ION INDIRECTLY?

Only the hydrogen-ion developed directly by water in the soil can have any influence on the growth of plants; for the latter have no clairvoyant powers, and can not respond in any way to acidity which does not exist, but which the soil has merely the ability to produce when treated with certain chemical substances. Since, however, writers on soil acidity often overlook this fact, and discuss indirectly-produced acidity as if it affected plants, and since many of the methods proposed for determining "lime-requirement" are based on the measurement of this type of acidity, the indirect production of acidity will be discussed in outline here.

When a solution of a neutral salt, like calcium chloride, is added to a soil, the solution becomes more or less strongly acid. This is not the result of a single process, but is the combined effect of several, including the following:

Double Decomposition.—Aluminium silicate plus calcium chloride yields calcium silicate plus aluminium chloride; the last, being a salt of strong acid with a weak base, yields hydrogen-ion, and hence an acid reaction, to the solution.

Replacement of Ions.—Calcium ion from the solution may replace aluminium ion present in an adsorbed form on the surfaces of the particles of the soil colloids, the net result being essentially the same as in the preceding paragraph. Calcium ion may also replace hydrogen-ion adsorbed on the colloids, whereupon the solution will become acid; this is quantitatively by far the most important source of indirect acidity.

Coagulation of Colloids.—Calcium chloride and other salts have the power of coagulating colloids, and reducing correspondingly their power of adsorption; acidity may be produced by the ions thus set free just as in preceding instances.

The first of these processes is to be expected only with the clayey matter in the soil, but the other two apply to both clay and humus. The more colloidal material a soil contains the greater is likely to be the acidifying effect of adding a neutral salt.

HOW CAN THE CAUSE OF SOIL ACIDITY BE RECOGNIZED IN A GIVEN CASE?

The acidity of a soil may be due to the simultaneous presence of so many different substances that no general procedure for the identification of individual ones can be formulated. The following plan, however, permits of the recognition of whether the principal acid present is highly, moderately, or only slightly, ionized.

Stir up about 25 grams of soil with 50 c.c. of distilled water, allow to settle, and decant the liquid upon a small filter paper, throwing away the first few c.c. coming through (since they contain traces of acid extracted from the paper). Test the acidity of the filtrate by placing 1 cc. of it in a test tube and adding a drop of methyl red indicator; if its least acid color, yellow, is shown, repeat with brom-cresol purple indicator. Prepare a solution of hydrochloric acid of such dilution that 1 c.c. of it gives with the same indicator a color exactly matching that produced by the soil extract. Then prepare a solution of sodium hydroxide about 10 times as strong, on the molar basis, as is the acid.

Into two similar beakers place 10 cc. each of the soil extract and the acid solution, and add an indicator which shows its color changes at the physico-chemical neutral point, such as litmus or the more brilliant brom-thymol blue. Titrate both solutions with the sodium hydroxide solution. If both require approximately the same quantity of this alkali, the acidity of the soil is chiefly due to the presence of an acid comparable in strength—that is, in degree of ionization—to hydrochloric acid. If twice as much alkali is required for the soil extract as for the hydrochloric acid solution, then the acidity is chiefly due to a moderately strong acid, such as, for instance, lactic acid. If several times as much alkali is required for the soil extract as for the hydrochloric acid solution, then a weak acid is concerned in the production of the soil acidity.

The writer has tried this method with several acid soils, and has found the results to indicate the presence of moderately strong acid substances.

How Can Soil Acidity be Measured?

In order to have a basis for discussion, it will be desirable to tabulate the methods which have been suggested, in more or less chronological sequence, bringing together related ones.

Table 5. *Methods of measuring acidity present and producible in soils*

1. A salt solution is added to the soil; for this purpose there have been used: sodium chloride, potassium chloride and nitrate, calcium chloride, nitrate and acetate, zinc sulfide plus calcium chloride, etc. The quantity of acid in the resulting solution, which represents that originally present in the soil plus a much greater amount produced indirectly by the processes outlined on a previous page, is then determined by titration or other means.
2. No salt solution, but some pure water, is added to the soil.
   A. The mixture is titrated with lime water, using either an indicator, or observation of the freezing point, to determine the end point. This gives the amount of lime needed to neutralize the acid originally present in the soil plus that produced indirectly by the action of lime (which is likely to differ from that produced by a neutral salt solution) as well as the amount of lime required to satisfy the adsorptive power of the soil colloids for calcium ion under the given conditions.
   B. The mixture is filtered, and the filtrate titrated with standard alkali. This gives the quantity of acid present in the soil.
   C. The hydrogen-ion concentration or specific acidity is determined:
      a. By catalysis of an ester.

b. By measurement of the potential due to hydrogen-ion with the potentiometer.

c. By observation of color changes of indicators whose relations to hydrogen-ion concentration are known.

From the discussion of the indirect production of acidity in soils already given it is evident that the methods listed under 1 in Table 5 are *not* methods of determining the acidity originally present in a soil. The results they yield are composite, representing both acid originally present and a usually greater quantity produced by the treatment. That the results obtained would differ widely with the salt used and with the conditions of the experiment would naturally be expected, and has been demonstrated by actual trial.[8] Even when soils are neutral or alkaline at the start they may develop a considerable acidity when treated with a salt solution; and any method which indicates an alkaline soil to be acid is certainly valueless for the determination of the effect of acidity on plant growth.

By way of analogy, suppose a man has one pocket full of coins, and another full of slugs. In so far as his ability to purchase commodities is naturally be expected, and has been demonstrated by actual trial.[8] Even though the slugs can, by appropriate procedure, be converted into coins, they have only potential and no direct purchasing power. Determination of the total number of metal objects, or of the total weight of metal, which the man carries, can of course be carried out with as high a degree of precision as desired; but what bearing will this data have on his actual wealth?

While some writers erroneously regard these methods as yielding values for soil acidity, others merely claim them to be "lime-requirement" methods, this term being understood to refer to the amount of lime which must be added to the soil per acre-foot (or other unit of area and of depth) to render its reaction neutral. The amount of lime needed to neutralize the acidity of a solution produced by the action of an arbitrarily selected salt upon a soil is, however, not necessarily related in any way to the amount of lime which would be needed to neutralize the soil when applied directly (as described under *2 A,* in Table 5). It is therefore also erroneous to term these methods lime-requirement methods.

Since the methods in this group yield composite, variable, and contradictory results, and furnish no information as to the soil acidity nor as to the lime-requirement, it can only be concluded that they are valueless in connection with any study of soils in relation to plant growth.

The writer is impelled to make these strong statements because of the appalling amount of time and energy which is being expended in applying these salt-solution acidification methods. Articles are continually being published, in which important conclusions as to relations between soils and plants are based on results obtained by them; and commercial organizations are putting on the market apparatus for carrying them out. It is hoped that the present paper will at least lead future workers to reflect upon the significance of any proposed method of studying soils, before deciding to adopt it.

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[8] Ames and Schollenberger, Journ. Ind. Eng. Chem., **8**: 243. 1916; under some conditions different salts may yield, however, approximately the same result: Knight, Journ. Ind. Eng. Chem., **12**: 340. 1920.

Taking up now the methods listed under 2 *A,* in Table 5, it may be stated that the lime-water (Veitch) method gives directly the amount of lime needed to bring the soil to the degree of acidity or alkalinity shown by the indicator used. If phenolphthalein is selected, the result is the amount of lime which will give the soil a specific alkalinity of 30. If, however, litmus or brom-thymol blue were to be used, the amount of lime required to render the soil neutral would be obtained. This method, then, though obviously not permitting the determination of soil acidity, is ***a real lime-requirement method.*** If the freezing point of the soil solution is used to indicate the course of the titration, it may be possible to recognize individually the point at which acid is neutralized as well as that at which lime ceases to be taken up by the soil; so that this method is capable of yielding both quantity of acid and lime-requirement.

The method given under 2 *B,* in Table 5, permits the determination of the *quantity* of acid present in a given soil in the simplest possible way. An indicator whose color changes occur at the neutral point should, however, be used. Neither methyl orange nor phenolphthalein, however useful they may be for obtaining comparative results in ordinary titrations, shows when a solution has been actually neutralized. When an acid solution is being titrated, the former changes its color long before the neutral point has been reached and the latter does not begin to change until well past neutrality.

For reasons already explained in detail, the quantity of acid present in a soil is far less significant than the hydrogen-ion concentration or specific acidity, when effect upon the growth of plants is under consideration. The methods under 2 *C,* in Table 5, are therefore the only ones which should be used in studying this subject. Method *a* is difficult to apply and to interpret. Method *b* is justly resorted to for testing soils where the necessary apparatus is available. A portable apparatus, suitable for determining the electrical potential of soil solutions in the field has recently been designed by Professor S. F. Acree and collaborators,[9] and should prove very useful for work of this sort.

FIELD METHOD OF MEASURING SOIL ACIDITY

The indicator method, *c,*[10] while less accurate than the potentiometer method is, however, so simple to apply that it can be recommended for use in all ordinary studies of soil acidity in relation to plant growth.[11] Under the most favorable conditions it is possible by the indicator method to measure acidity and alkalinity with much greater precision than is necessary in the field. By treating the indicators with buffer solutions of known ionic concentration, many hues intermediate between those in the accompanying color chart can be distinguished. On comparing the colors thus produced with those developed by mixing clarified soil extracts with the same indicators, specific acidities differing by a factor of $\sqrt[5]{10}$ or 1.59 ($P_H = 0.2$) can be recognized. In the field, where it is inconvenient to carry buffer solutions to prepare standards for comparison, and where the turbidity of soil extracts is difficult to remove, it is impracticable to work closer than values differing by a factor of $\sqrt{10}$ or 3.16 ($P_H = 0.5$) which is rounded off for simplicity to 3+. This degree of precision is, however, entirely adequate for the purpose in view, for it has been repeatedly found that from one to another plant of the same species, or indeed, from one to another root on the same individual, separate observations of reaction may differ by a factor of 10 or more.

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[9] For sale by the Will Corporation, Rochester, New York.

[10] Clark and Lubs, Jour. Bacteriology, 2: 1, 1917; Gillespie, Jour. Wash. Acad. Sci., 6: 7, 1916.

The following outfit is used.[12] First, a rectangular box about 3.5 × 5 × 9 cm. in dimensions. In the box, six vials for the indicators, 1.5 × 5.5 cm., capacity 8 c.c., each provided with a cork or rubber stopper, into which is inserted a glass rod flush with the top of the stopper, and extending nearly to the bottom of the vial; to prevent undue compression upon inserting the stoppers, a groove may be cut in the side of each, so as to reach nearly to the lip of the vial. Then, three or four vials in which to extract the soils, about 2 × 5 cm., made of heavy glass, to prevent undue breakage; a container for water, which may conveniently be a screw-capped jar holding 200 c.c. or more, or an aluminum canteen; and a pipette, most simply constructed of two pieces of glass tubing a few cm. in length, connected by a rubber tube.

The six indicators which have proved most satisfactory in work with soils are: bromphenol blue, bromcresol purple, bromthymol blue, phenol red, methyl red, and *o*-cresolphthalein or phenolphthalein. The first three are used, as recommended by Clark and Lubs,[13] in about 1 percent solution in water, titrated with dilute sodium hydroxide to their intermediate colors; and the phenol red in a 0.5 percent solution similarly titrated. The methyl red and phenolphthalein are used as 0.05 percent solutions in 50 percent alcohol. It should be noted here that litmus paper, which is often recommended for testing soil reaction, is much less sensitive than the above indicators, and may give misleading results.[14]

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[11] The following description is reproduced, with minor modifications, from the Jour. Wash. Acad. Sci., 10: 217, 1920.

[12] Sets of indicators similar to that here described are for sale by the La Motte Chemical Products Co., 13 W. Saratoga St., Baltimore, Md.

[13] Journ. Bacteriology, 2: 135. 1917.

A simplification of the procedure previously recommended has been adopted; modifications may still be desirable in special cases. But before giving the directions, a word should be added concerning the water used for mixing with the soil. If calcium bicarbonate is present in this water, the soil acidity will be diminished; while if neutral salts, such as sodium chloride, and especially calcium sulfate, are present in any considerable amount, the acidity will be appreciably increased. The former effect is a direct neutralization; but the latter is due to the fact that the clay and the humus[15] in the soil adsorb the basic elements from neutral salts, and set the acid free. In the laboratory, distilled water can be used, and, to attain the greatest precision, air freed from carbon dioxide can be blown through it until it reacts quite neutral; when one is traveling, distilled water can usually be purchased from a drug store, and will give satisfactory results without special purification. In the wilds the best that can be done is to obtain spring or well water rising through rocks as free as possible from soluble constituents—such rocks as sandstone, shale or schist. In calcareous regions it may be necessary to test waters from one source after another until a sample is found which reacts neutral—is colored green by a drop of bromthymol blue indicator—and to arrange the trip so that the water supply can from time to time be replenished from this source.

With these points in mind, the following approximate directions have been drawn up:

A sample of soil a gram or two in weight is shaken from living roots into an empty vial, and 5 c.c. of the most nearly neutral and salt-free water available is added, the vial being shaken well to insure complete mixing. After the soil and water are thoroughly mixed, the solid matter may be compacted with a glass rod or a stick, and the vial then supported at an angle of 45° and allowed to stand until the bulk of the suspended matter has settled. The more or less clear liquid is then decanted or pipetted off into another vial, a drop or two of bromthymol blue or one of the other indicators, the color changes of which occur near the neutral portion of the table, are added, and the color assumed is noted. If either of the extreme colors is shown, the process is repeated with the indicator whose color changes come next in the corresponding direction; and this is continued until either an intermediate color of one indicator, or opposing extremes of two overlapping ones, are obtained, whereupon the specific acidity or alkalinity can be read off from the chart.

The more turbid the liquid, the more indicator must be added, and the less certain are the results obtained. The turbidity can, of course, be re-

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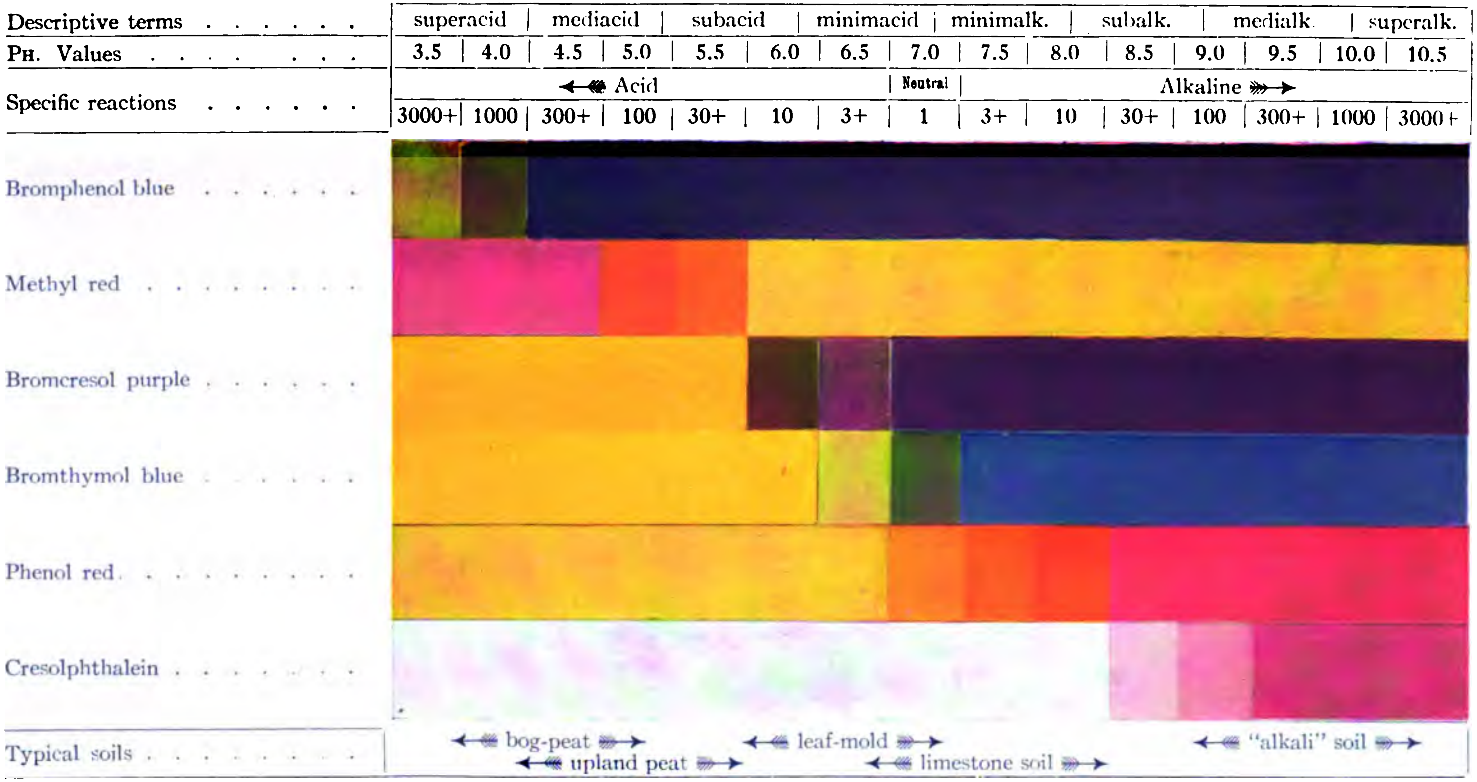
[14] Gillespie and Wise, Journ. Amer. Chem. Soc., 40: 796. 1918.

[15] Gillespie and Wise, op. cit.

CHART SHOWING COLORS OF INDICATORS USED FOR DETERMINING SOIL REACTIONS.



Descriptive terms	superacid		mediacid		subacid		minimacid		minimalk.		subalk.		medialk.		superalk.
PH. Values	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5
Specific reactions			← Acid					Neutral				Alkaline →			
	3000+	1000	300+	100	30+	10	3+	1	3+	10	30+	100	300+	1000	3000+

DIRECTIONS: To determine the specific acidity or alkalinity of a soil extract with the aid of this table, add first a drop bromthymol blue. If the liquid is colored green, the reaction is neutral; if yellow, it is acid; if blue, alkaline. If acid, repeat with successive indicators lying above bromthymol blue; if alkaline with those lying below. Continue until either an intermediate color of one of these indicators, or opposing extremes of two overlapping ones, are obtained. The specific acidity or alkalinity can then be found at the head of the corresponding column.

moved by the addition of coagulating agents or by filtration through paper; but it is essential to make certain that these do not in themselves show an acid or an alkaline reaction. The most satisfactory results of all can be obtained by running a quantity of the soil through a paper filter until two successive portions yield the same value when tested with indicators. But such procedures are more suited to laboratory than to field studies, and after a little experience one can tell the indicator color-change with certainty, even in the presence of considerable brown mud.

To illustrate the procedure followed in actual practice, two typical cases encountered by the writer may be cited here.

1. A black soil in pockets in limestone rock, supporting spleenwort ferns, was treated as above, and on testing the soil extract with bromthymol blue indicator, a strong blue color was obtained; reference to the chart showed that the reaction must be alkaline, and the value of specific alkalinity 3 or more ($P_H = 7.5$). The process was repeated with the indicator, the color changes of which lay next toward the alkaline side of the table, namely, phenol red. With this indicator a clear red color was obtained, showing the reaction to be actually specific alkalinity 10 ($P_H = 8.0$).

2. Soil from a dry blueberry thicket was tested, and, since upland peat is usually distinctly acid, the first indicator tried was bromcresol purple, the color changes of which occur just to the acid side of the neutral point; with this indicator a yellow color was obtained, indicating a specific acidity of at least 30. The soil was accordingly tried again with methyl red, which lies next toward the acid side, and this gave a violet-red color, corresponding to a specific acidity of 300 or more. It was accordingly necessary to try an indicator working at still higher acidities, namely bromphenol blue; and this yielded a violet color, indicating 300 or less. The last two indicators agreed, then, in fixing the reaction of this soil as: specific acidity 300 ($P_H = 4.5$).

In spite of certain limitations, this method is capable of giving definite information as to soil reaction in many cases. And the results obtained by the writer on a number of species of native plants, described in other communications,[16] have been of such significance that the method is published for the benefit of students of plant distribution and others interested in soil acidity and alkalinity.

[16] Ecology, Vol. I, No. 1, pp. 42–48, 1920; Rhodora, 22: 33, 1920; Am. Fern. Jour. 10: 15 and 46, 1920; Proc. Acad. Nat. Sci., Philadelphia, 1920: 84 and 113.

SOME RELATIONS BETWEEN ANTS AND FUNGI

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The remarkable fungus-growing and fungus-feeding habits of the neotropical Attiine ants, first surmised by Belt (1874) and Fritz Müller (1874) and subsequently elucidated by the classical investigations of Tanner (1892), Alfred Moeller (1893), Huber (1905) and Wheeler (1907), have led to a search for other fungivorous representatives of the Formicidæ.

Emery (1899) is of the opinion that *Messor barbarus* subsp. *structor* Latr. feeds upon fungi, as well as seeds and other food-substances. Lagerheim (1900) states that *Lasius fuliginosus* Latr. cultivates *Cladotrichum myrmecophilum* (Fres.) Lag.,[1] which functions as a food and in giving stability to the walls of its carton nest. Ferdinandsen and Winge (1908) quote Raunkiaer as having reached the conclusion that *Chromosporium formicarum* Ferd. & Wge. is eaten by the ants in whose nest it grows. Farquharson (1914) appears to favor the view that certain Nigerian Crematogasters are fungus-farmers. Donisthorpe (1915) believes that *Cladosporium myrmecophilum* (Fres.) Ell. is an important item of food in the diet of *Lasius fuliginosus,* and that *Hormiscium pithyophilum* (Wallr.) Saccr. var. *myrmecophilum* Ell. is cultivated by *L. umbratus* Nyl. Elliott (1914) suggests that the "pure cultures" of fungi in the carton nests of *L. fuliginosus* and *L. umbratus* probably originate—as is the case with fungi cultivated by certain Attiine ants—by a transfer of a definite culture of mycelium which is subsequently manured, tended and weeded by the ants.

The principal arguments advanced in favor of the view that various Formicidæ, other than the Attii, cultivate and feed upon fungi are the following: (1) The association of a particular fungus with a particular species of ant, (2) the occurrence of the fungus in "pure cultures," (3) the cropping of aerial and other hyphæ by the workers and, (4) analogies with the fungus-growing and fungus-feeding habits of the Attiine ants. It is to be emphasized in this connection, however, that the occurrence of more or less pure cultures of a particular fungus in the domatia of a given species of insect, does not indicate necessarily that the mycelium is actually cultivated and eaten by the latter, since, as suggested by Perkins (1914), the mats of hyphæ may be adventitious. Nor is the cropping of aerial hyphæ conclusive evidence that a fungus is eaten by an insect. Miehe (1911) found localized, luxuriant growths of certain fungi in the pseudo-bulbs of the myrmecophytic Hydnophytum and Myrmecodia, but concluded that the aerial hyphæ are cropped by the ants merely to prevent them from obstructing the galleries. Furthermore, it must be admitted that there is a considerable element of uncertainty in reasoning, from analogy with the highly specialized, phytophagous Attii, that representatives of the cosmopolitan, more or less omnivorous Crematogastrii, Formicii, etc., are fungus farmers.

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[1] Elliott (1914) considers that this fungus is not a *Cladotrichum* and refers it to *Cladosporium myrmecophilum* (Fres.) Ell.

Relations between Ants and Fungi in Myrmecophytes

Recently, I have devoted considerable attention to the study of an interesting group of African myrmecophytes.[2] These ant-inhabited plants, which belong to three distinct orders, Parietales, Tubifloræ and Rubiales, are characterized by an inherent tendency towards the formation of a heterogeneous pith, the central succulent portion of which collapses and dries up, leaving an internal chamber or cavity which is taken possession of by ants and used as a domatium. In certain of the Ethiopian myrmecophytes, species of Cuviera, Plectronia and Sarcocephalus and *Barteria fistulosa* Masters, the internal cavities tend to be localized in certain shoots or particular portions of the stems and branches, and are concomitants of more or less pronounced hypertrophies of these organs; whereas in others, *Vitex Staudtii* Guerke and *Barteria Dewevrei* De Wildeman & Durand, the phenomenon is less localized and there are no external indications of swellings or enlargements of the stems and branches. All of the myrmecophytes differ from previously described extra-African myrmecophytic plants in the occurrence within their myrmecodomatia of excavations which contain peculiar callus-heteroplasias. These traumatic structures, zoöcecidia, are arranged more or less symmetrically in relation to the phyllotaxy of the plants, and are formed by the young cambium and cortex when these tissues are exposed by the removal of the underlying cells of the medulla and xylem. In endeavoring to trace the various stages in the development of the zoöcecidia, and to account for their symmetrical distribution in relation to phyllotaxy, I have had occasion to section a considerable number of myrmecodomatia and to study the minute anatomy of various extra-Ethiopian myrmecophytes for purposes of comparison.

All of the ant-inhabited plants (species of Acacia, Triplaris, Cecropia, Nauclea, Enterolobium, Myrmecodia and Hydnophytum, as well as Cuviera, Vitex, Plectronia, Barteria and Sarcocephalus) of which I have succeeded in obtaining suitable material[3] have a more or less luxuriant growth of fungi upon the inner walls of their myrmecodomatia. The mycelia are sporadically distributed in most cases, but their aerial portions show unmistakable evidences of having been cropped by the ants. In three of the myrmecophytes, *Plectronia Laurentii* De Wildeman[4] and *Cuviera angolensis*[4] Hiern. and undetermined material of the latter genus[5] there are dense mats of delicate, white hyphæ which resemble "ambrosia." These mycelia are confined to the two concave ends of the spindle-shaped domatia. As shown in figure 1, the aerial hyphæ project from a dark colored substratum which rests, in turn, upon medullary tissue. When macerated, the dark colored layer is found to be composed of the detritus of the ant colony, *i.e.*, fecal substances, disintegrated pellets, etc. The mycelium radiates through this detritus in all directions and penetrates into the superficial layer of medullary cells.

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[2] Bailey, I. W., "The Anatomy of Certain Plants from the Belgian Congo, with Special Reference to Myrmecophytism," Bull. Am. Mus. Nat. Hist. Ined.

[3] The bulk of the material consisted of freshly killed speimens preserved in 70–90 percent alcohol.

The questions suggest themselves, accordingly, (1) are the mycelia, which occur in the various myrmecodomatia and are cropped by the ants, eaten by them, and (2) are they cultivated by the ants or merely adventitious?

Of course, there are serious obstacles in the way of securing observations upon the normal activities of ants in myrmecophytes, even when living plants and insects are available. In dealing with other groups of animals, under somewhat similar circumstances, investigators have resorted to analyses of fèces or the contents of alimentary tracts. Although ants are supposed to take only fluid or semifluid substances into their crops and stomachs, they have a curious infrabuccal chamber, into which pass fragments of animal and plant tissues upon which they are feeding. The material that accumulates in this cavity—in the form of a pellet—is finally cast out or fed to a larva (Pseudomyrminæ).

A number of the pellets of the Crematogasters which inhabit the myrmecophytic Cuvieras are composed entirely of fragments of the ambrosia-like mycelia (fig. 2). Furthermore, the infrabuccal chambers of the ants[6] which inhabit the other myrmecophytes contain numerous fragments of aerial hyphæ (fig. 4), which appear to have been removed from the walls of the domatia. Although such facts as these might be considered to indicate that the ants feed to a greater or less extent upon the fungi, they afford no clue in regard to our second question. There are, however, certain general phenomena which are worth recording in this connection.

The environment in the interior of the myrmecodomatia is usually very favorable to the growth of fungi. The walls of the domatia are commonly excellent "culture-media" and the equable temperatures of the moist, dark chambers facilitate the germination of spores and the growth of mycelia.

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[4] Inhabited by *Crematogaster africana* subsp. *laurenti* var. *zeta* Forel.

[5] Inhabited by *C. impressiceps* var. *frontalis* Santschi (var. nov.).

[6] Species of *Pachysima, Pseudomyrma, Azteca, Viticicola, Crematogaster* and *Camponotus.*

Under these circumstances, it is almost inevitable that the nests should become infected with fungi; for not only do the ants transport spores, which become accidentally attached to their bodies and appendages, but their pellets contain numerous spores[7] of different kinds, the most resistant types of which probably remain viable. The growth and sporadic distribution of the hyphæ in most of the myrmecodomatia suggest that the mycelia are purely adventitious. Only in the case of the localized luxuriant growths of "ambrosia" in *Cuviera* and *Plectronia* are there indications that the ants may actually be fungus-farmers; *i.e.*, the mycelia appear to me more or less pure cultures and are closely associated with the detritus of the ant colonies.

Von Ihering (1898) and Huber (1905) have shown that the *Atta* queen, during her nuptial flight, carries a culture of mycelium in her infrabuccal sac, which is deposited in the new nest, fertilized with liquid feces and triturated eggs, and carefully tended first by the queen and subsequently by the incipient colony. The walls of recently occupied myrmecodomatia of *Cuviera* are covered with aerial hyphæ (fig. 3). As the colony increases in size, the walls are scarified and the hyphæ cut away except at the ends of the domatia, where the detritus of the colony is deposited and the future "fungus-gardens" are located. It is conceivable, therefore, that the luxuriant growths of ambrosia may have originated in one of the following ways: (1) By the adventitious growth of some ubiquitous fungus which, in the peculiar environmental conditions within the myrmecodomatium, tends to become dominant and is finally confined to those portions of the nest where the detritus of the colony is deposited; (2) by a process of selective weeding on the part of the ants; (3) by the transfer of a definite culture of a particular fungus which tends to diffuse over the walls of the domatium until it can be confined, manured and weeded by the developing colony. It does not seem probable, however, that the facultative and more or less omnivorous Crematogasters have attained as high a degree of specialization in their relation with fungi as is essential if the latter solution is the correct one. Furthermore, it should be noted that frequently there is a tendency among ants to deposit their feces, the castings from their infrabuccal cavities, etc., in some more or less restricted portion of their domatia. These aggregations of partly digested animal and plant tissues naturally tend to give rise to luxuriant growths of fungi. Therefore, the fact that the dense mats of ambrosia rest upon detritus cannot be considered, in the absence of reliable collateral evidence, to indicate necessarily that the myeclia are actually manured and tended by the ants.

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[7] Many of the pellets contain, in addition to fragments of fungi and other substances secured from within the myrmecodomatia, much extraneous material, i.e. fragments of insects, bits of plant tissue, hairs, pollen, dirt, and large numbers of spores of many different kinds, fig. 5.

RELATIONS BETWEEN OTHER FORMICIDÆ AND FUNGI

The occurrence of large numbers of spores and fragments of hyphæ in the pellets of certain Pseudomyrminæ, Myrmicinæ, Dolichoderinæ and Formicinæ, which are "obligatory" or "facultative" inhabitants of various Ethiopian and extra-African myrmecophytes, raises the question, is this relation between ants and fungi an isolated phenomenon or one that is characteristic of other representatives of these subfamilies?

PSEUDOMYRMINÆ.—The strongly hypocephalic larvæ of Pseudomyrmine ants[8] are fed with pellets voided from the infrabuccal pockets of the workers. The pellets are inserted into a curious depression or pouch (trophothylax) which is located on the ventral surface of the larva close to its head. Owing to their relatively large size and dark color, these pellets are quite conspicuous and easily obtained from larvæ preserved in alcohol. My colleague, Professor W. M. Wheeler,[9] and I have recently analyzed more than 400 pellets of various Pseudomyrminæ. The larvæ, from which the pellets were taken, belonged to a number of different species and varieties of the four genera of this subfamily, and were collected at various seasons of the year in several localities in Texas, Mexico, Guatemala, Costa Rica, British Guiana, the West Indies, the Philippines and the Belgian Congo. As was to have been expected, *a priori,* in view of the well-known entomophagous habits of these ants, 85 percent of the pellets contain more or less numerous fragments of insects, *e.g.,* coccids, mites, spiders, beetles, larvæ, etc. (fig. 6). Although a number of these pellets, approximately 25 percent, are composed entirely of animal tissue, a majority, 65 percent, contain fungous spores and fragments of hyphaæ (fig. 9). Frequently the spores and hyphæ are so numerous as to form a large fraction of the total volume of the pellet. Furthermore, many of the pellets, which are devoid of animal tissue, are composed entirely of spores (fig. 8), or spores mixed with pollen (fig. 7). Usually the spores are of several distinct types (figs. 7, 11), but occasionally a pellet is encountered in which they are all, or nearly all, of one variety (fig. 8). The fungus-containing pellets are not confined to any particular groups of the Pseudomyrminæ, but occur in all species and varieties, regardless of the locality where they were collected or the nesting habits[10] of the ants.

The infrabuccal pockets of imagines, queens and workers contain the same assortment of substances as the larval trophothylaces, but usually in somewhat different proportions. In other words, they tend to have a smaller proportion of animal tissue. This is due, in all probability, to the fact that the worker-nurses add fragments of insects to their pellets before feeding them to the larvæ.

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[8] *Pseudomyrma, Pachysima, Tetraponera,* and *Viticicola.*

[9] Wheeler, W. M., and Bailey, I. W., "The Feeding Habits of Pseudomyrmine and other Ants," Trans. Amer. Phil. Soc. Ined.

[10] Nesting in the ground (*Pseudomyrma elegans* Sm.), in dead twigs (*Tetraponera, Pseudomyrma*) or in myrmecophytes (*Pseudomyrma, Pachysima, Viticicola*).

PONERINÆ, DORYLINÆ, MYRMICINÆ, DOLICHODERINÆ, AND FORMICINÆ. —More recently, the writer has dissected the heads of queens, males, soldiers and workers of various representatives of the Ponerinæ, Dorylinæ, Myrmicinæ, Dolichoderinæ and Formicinæ, and studied the contents of their infrabuccal cavities. The results of analyses of 736 pellets from 25 genera of the five subfamilies are recorded in the following table:

Ant	Locality	Nesting in	Food			
			Animal tissue	Plant tissue	Fungi	No pellets
PONERINÆ						
Myrmecia tarsata Sm.	N. S. W.	Ground	S	A	F–VN	14
M. gulosa Fabr.	N. S. W.	Ground	S–A	A	N–VN	8
Paraponera clavata Fabr.	Panama	Ground	S	A	VN	10
Diacamma australe Fabr.	Queensland	Ground	S	A	VN	16
Odontomachus hæmatoda L.	Costa Rica	Ground	S	A	N–VN	10
DORYLINÆ						
Dorylus anomma var. *nigricans* Illiger	Congo	Ground	A	?	F	18
Eciton burchelli Westwood	British Guiana	Ground	A	S	F–N	10
MYRMICINÆ						
Leptothorax curvispinosus Mayr	N. Y.	Dead twigs	?	A	N	41
Aphænogaster tennessensis Mahr.	Mo.	Rotten stumps and logs	?	A	N	30
Veramessor pergandei Mayr	Ariz.	Ground (H)	?	A	F	18
V. andrei Mayr	Calif.	Ground (H)	?	A	F	12
Pogonomyrmex barbatus Sm. var. *marfensis* Wheeler	Texas	Ground (H)	S	A	F–N	46
P. barbatus Sm. subsp. *rugosus* Em.	Ariz.	Ground (H)	S	A	F–N	42
Solenopsis geminata var. *rufa* Jerdon	P. I.	Ground (H)	?	A	N	6
S. geminata var. *diabola* Wheeler	Texas	Ground (H)	?	A	F–N	18
Myrmicaria eumenoides Gerst.	Congo	Ground	?	A	F–VN	12
Atta cephalotes L.	(3) Costa Rica	Ground	?	A	F–VN	22
Trachymyrmex septentrionalis McCook var. *obscurior* Wheeler	Florida	Ground	?	A	F–N	8
Cryptocerus multispinus Em.	Guatemala	Dead branches	S	A	F–VN	8
DOLICHODERINÆ						
Liometopum apiculatum Mayr	Ariz.	Carton nests in hollow live oaks	?	A	F–N	10
L. occidentale Em.	Calif.	Carton nests in hollow live oaks	S–A	A	N–VN	18
Leptomyrmex nigriventris Guérin	N. S. W.	Hollow logs	S	A	N–VN	14
Dolichoderus doriæ Em.	N. S. W.	Ground	S–A	A	F–VN	19
Azteca instabilis Sm.	Guatemala	Carton nest	S	A	VN	24

FORMICINÆ

Ant.	Locality	Nesting in	Food			
			Animal tissue	Plant tissue	Fungi	No. pellets
Œcophylla longinoda Fabr.	Congo	Silk and leaf nests on trees	S	A	N	16
Lasius fuliginosus Latr.	Switzerland	Carton nests hollow trees	?	S	VN	33
L. interlectus Mayr	Ill. and Colo.	Ground	?	A	F–N	12
Formica rufa L. var. *obscuripes* Forel	B. C.	Mound nests	?	A	F–VN	17
Myrmecocystus melliger Forel	N. Mex.	Ground	?	A	F	12
Camponotus maculatus Fabr. subsp. *McCooki* Forel var. *sansabeanus* Buckley	Texas	Ground	A	S	F–N	11
C. brutus Forel	(3) Congo	Rotten wood	S	A	VN	50
C. sericeiventris Guérin	Guatemala	Rotten tree trunks	?	A	VN	35
C. acutirostris Wheeler	Ariz.	Ground	S–A	A	F	7
C. herculeanus L. subsp. *ligniperda* Latr. var. *novaboracensis* Fitch	(2) N. Y.	Decaying stumps	S	A	N	41
C. abdominalis Fabr. var. *costaricensis* Forel	Costa Rica	Dead trees	S	A	N–VN	17
C. nigriceps Sm.	Queensland	Ground	A	A	F–VN	18
Polyrhachis dives Sm.	P. I.	Silk and detritus nests on trees	A	A	F–VN	10
P. ammon Fabr.	N. S. W.	Ground	S–A	A	F–VN	23

S = fragments of tissue scanty.
A = fragments of tissue abundant.
F = spores or fragments of hyphæ infrequent.
N = spores or fragments of hyphæ numerous.
VN = spores or fragments of hyphæ forming considerable fraction of total volume of pellet.
H = seed-storing ants.

It is significant that fragments of insects, such as are present in the infrabuccal sacs of Pseudomyrminæ, are of infrequent occurrence except in the pellets of Dorylinæ, *Myrmecia gulosa, Liometopum occidentale, Dolichoderus doriæ Camponotus maculatus* var. *sansabeanus, C. acutirostris, C. nigriceps* and *Polyrhachis*. On the other hand, vegetable substances are almost invariably present except in the Dorylinæ.

The pellets tend to contain more or less numerous spores and fragments of hyphæ. This is as true of the supposedly primitive, entomophagous Ponerinæ as of the more or less omnivorous Myrmicinæ, Dolichoderinæ and Formicinæ; of ants of temperate as of tropical regions; and of species which nest in the ground or in carton or silk domatia, as of those which live in decaying plant tissue. As shown in the sixth column of the table and in Plate VI many of the ants have pellets that contain large numbers of spores—usually of several (3–12) distinct types—and numerous fragments of hyphæ. Occasionally a pellet is encountered which is composed entirely of fungus filaments and spores, but usually there are present at least a few bits of sound or decaying plant tissue. I have found very few pellets that are entirely devoid of fungi, except among the Dorylinæ, Veramessor, Pogonomyrmex, Myrmecocystus and *Camponotus maculatus* var. *sansabeanus*. However, even the harvesting ants, which live in relatively xerophytic environments, frequently have numerous spores and bits of chromogenic hyphæ in their infrabuccal chambers.

It is evident, accordingly, that there is a general tendency among ants for the imagines to take spores and fragments of myeclia, or bits of decaying plant tissue, into their infrabuccal pockets. What then is the significance of this generalization? Are most Formicidæ fungivorous? The answer to these questions depends upon the function of the infrabuccal chamber, whether it is actually a receptable for nutritive material or a sort of cephalic dustpan for accumulations of food-residues and detritus.

Structure and Function of the Infrabuccal Cavity

The infrabuccal cavity of wasps was studied by Brants (1841), who came to the conclusion that it functions as a receptacle for materials used in the construction of carton. This supposition was criticised by Meinert (1860). He was inclined to believe that the "mouth-sac" of ants and wasps serve as a crop or "social stomach." Adlerz (1886) rejected Meinert's explanation, but offered no substitute hypothesis. Lubbock (1877) devoted considerable attention to the study of the anatomy of the mouth-sac. He states:

> "In the posterior wall of the mouth is an orifice which leads into a large lobular sac. . . . Its membranous walls appear to be firm and elastic. I have not found any muscles attached to it, and presume that it is kept open by the elasticity of the walls. The orifice of the mouth sac can be closed at will by a small flap which is supplied with several muscular fascicles. The cavity generally contains a brown, spongy mass. . . . In ants, as it seems to me, the general action of the muscles which open the pharynx would tend to empty the mouth sac; those which draw down the lower wall of the pharynx, by directly constricting the mouth sac, while even those attached to the upper wall of the pharynx would tend to empty the mouth sac by sucking out its contents. . . . In fact, as it seems to me, the contents of the mouth sac are not intended only to pass outwards through the mouth, but, on the contrary, into the œsophagus through the pharynx."

Janet (1895*a*, 1895*b*, 1896, 1897) appears to be the only student of ants who has studied the function of the infrabuccal sac with any degree of care. He endeavored to prove, by feeding experiments in artificial nests and by dusting ants with various powders, that the infrabuccal pellets are composed either of food-residues or dust and detritus (which the imagines remove by means of their toilet-organs from their own bodies, from their progeny and from their companions) or a mixture of these two classes of substances.

> "Au-dessus du labium il y a une cavité supralabiale, de forme arrondie, dans laquelle les matières pulpeuses râpées, plus ou moins comprimées, abandonnent les liquides qui sont absorbés comme nourriture et laissent, comme résidus, les parties solides trop grossières qui sont rejetées moulées en petits corpuscules enroulés de forme caractéristique. Il suffit de donner, par exemple à des *Lasius fuliginosus* que l'on vient d'installer dans un nid artificiel, une mangeoire garnie d'un mélange de miel et d'amidon pour trouver, quelques heures après, tout autour de la mangeoire, un bon nombre de ces petits corpuscules. C'est au-dessus de cette cavité de moulage des déchets et détritus solides que se trouve l'orifice buccal proprement dit" (1896, p. 15).
>
> Si l'on saupoudre des Fourmis (*Myrmica*) avec du tournesol bleu en poudre fine, elles s'en débarrassent assez vite. On constate d'abord qu'elles circulent pendant quelques instants dans la boîte sans faire aucune tentative de nettoyage. Mais bientôt elles font passer leurs antennes dans l'organe pectiné, puis elles nettoient ce dernier en faisant passer leurs pattes entre les mandibules et les mâchoires. Au bout de quelques heures, on retrouve cette substance sous forme de petits grains, bleus, assez lisses et légèrement adhérents au verre. . . . Les Fourmis grattent avec leurs mandibules le gypse coloré en rouge qui constitue leur nid et elles se salissent avec la poussière ainsi produite. On retrouve, dans ce cas, le produit du nettoyage de leur corps sous forme de grains semblables aux précédents, mais rouges et granuleux (1895*a*, p. 697).
>
> "Comme les Fourmis, le Frelon nettoie ses antennes et d'autres parties de son corps avec ses peignes tibio-tarsiens. Les détritus ainsi enlevés sont repris par les peignes du promuscis et, finalement, emmagasinés dans la cavité supralabiale où il est rare de n'en pas trouver une petite quantité. Ils restent là et s'accumulent, jusqu'au moment où ils seront rejetés, comme partie intégrante d'un corpuscule enroulé. On peut voir les Frelons rejeter un semblable corpuscule presque chaque fois qu'ils terminent un repas sur du miel granuleux. Ils avalent la partie liquide et emmagasienent, dans leur cavité supralabiale, les granulations solides" (1895*b*, p. 108).

In dissecting queens, males, soldiers and workers of various representatives of the Ponerinæ, Dorylinæ, Pseudomyrminæ, Myrmicinæ, Dolichoderinæ and Formicinæ, and removing their pellets, I have had the opportunity of studying the anatomy of the infrabuccal pocket and its relation to other organs and tissues in the imaginal head. There appears to be no system of muscles or other visible mechanism for actually crushing, grinding or expressing liquids from the infrabuccal pocket. Furthermore, there are no glands which feed directly into it. If it is periodically flooded with granular secretions, they must drain or be forced into it from the pharynx or labium. There is no evidence, however, to indicate that the ants are able to digest any considerable portion of the more or less finely divided solid substances that are taken into the infrabuccal sac. The cells in voided pellets still retain their contents (starch, protoplasm, nuclei, etc.) and do not appear to have been acted upon by secretions from salivary or other glands. In fact, my observations favor Janet's contention that the function of the sac is to serve as a receptable for food-residues and detritus; or at least may be explained most satisfactorily upon the basis of such an assumption. Thus, the pellets of ants which nest in or travel over the ground contain much mineral matter, sand, dirt, etc. (fig. 13). On the other hand, the pellets of ants which excavate in sound or decaying twigs, stems, logs, stumps or roots, or utilize malaxated plant tissues in the construction of mounds or carton nests, have a relatively large admixture of vegetable débris. For example, as shown in figure 14, the pellets of *Camponotus herculeanus* subsp. *ligniperda* var. *novaboracensis* are composed principally of fragments of the thick-walled, heavily lignified tracheids and ray-parenchyma of *Thuja occidentalis* L. The infrabuccal sacs of *Leptothorax curvispinosus, Aphænogaster tennesseensis, Camponotus brutus, C. sericeiventris,* and *C. abdominalis* var. *costaricensis* usually are more or less completely filled with fragments of the moribund plant tissues in which the galleries and domatia of these ants are excavated. In a similar manner, the pellets of *Azteca xanthochroa, Pachysima æthiops, P. latifrons, Viticicola tessmanni,* and various species of *Crematogaster* and *Pseudomyrma* which inhabit myrmecophytes, contain a large admixture of triturated medullary and other tissues from the scarified walls of their domatia. When an ant has eaten or dismembered an insect, the infrabuccal sac tends to contain bits of chitin, hairs, scales, mandibles, tracheæ, etc., but few fragments of softer and more nutritious tissues.

That the infrabuccal cavity does not function as a receptacle for food, which is to be acted upon by saliva and other glandular secretions, is indicated, furthermore, by the composition of the pellets of the Attiine and seed-storing ants. Although the former are known to feed upon "kohlrabi" or "bromatia," and the latter large upon seeds, the infrabuccal pellets (that I have analyzed) seldom contain any considerable quantity of these food substances. The pellets of the Attii are composed largely of dirt, plant and animal hairs, bits of epidermal and other plant tissues, fragments of chromogenic hyphæ, spores, pollen, etc. (fig. 12); those of the harvesting ants largely of sand (fig. 13), dirt, bits of seed-coats, husks and other resistent plant tissues, fragments of dark-colored hyphæ, spores, hairs, etc. Occasionally, the infrabuccal chambers of the harvesting ants contain large fragments of seeds, but none of the pellets of the Attii that I have analyzed contain more than a few small bits of delicate, white hyphæ. It is of interest, in this connection, that the investigations of Moggridge (1873), Emery (1912) and others indicate that the harvesting ants feed upon the non-starchy, fluid or easily soluble portions of seeds.

ARE THE FUNGI IN THE INFRABUCCAL SAC FOOD-RESIDUES OR DETRITUS?

The consensus of opinion among students of ants is that these insects do not masticate their food with their mandibles or maxillæ. The act of feeding consists in lapping or rasping nutrient substances with the roughened surface of the protrusible tongue. However, the mandibles are used in tearing the food into pieces of convenient sizes and in rendering available its softer and more nutritious portions. Thus, the infrabuccal sac may contain, in addition to detritus of different kinds and from different sources, two distinct types of food-residues: (1) coarse fragments, which adhere to the surfaces of the ants during the process of cutting up or dismembering the food, and (2) finely divided particles, rasped off by the tongue and segregated from the fluid or semifluid substances that pass into the crop.

My analyses show that the crops and stomachs of the imaginal ants do not contain spores or fragments of hyphæ. If the ants actually feed upon fungi, they must triturate the spores and mycelia, or compress them, and drain off their liquid or semiliquid contents. Under such circumstances, one should expect to find torn or ruptured spores and finely divided fragments of hyphæ in the infrabuccal cavity. This is not the case, however, in any of the pellets that I have analyzed. The spores and the fungus filaments still retain their protoplasmic contents. In fact, all of the evidence at hand indicates that they are detritus scraped from the bodies and appendages of the ants, rather than food-residues. This is true even in the case of *Lasius fuliginosus, Crematogaster africana,* subsp. *laurenti* var. *zeta,* and *C. impressiceps* var. *frontalis,* in whose domatia are found what appear to be "pure cultures" of particular fungi.

The structure and activities of ants are such that they inevitably must accumulate numerous spores upon the hairy surfaces of their bodies and appendages, just as they do dirt, pollen and other types of detritus. In addition, the environmental conditions within their domatia facilitate adventitious growths of fungi which must be kept within bounds by a constant cropping of the mycelia. Luxuriant growth of aerial hyphæ, if they do not actually occlude the galleries and domatia, form formidable entaglements, and are likely to interfere with the brood. Thus, small colonies of ants in artificial nests frequently are swamped by fungi whose rapid growth cannot be controlled by a limited number of workers. In scarifying, cleaning and smoothing the walls of their domatia, ants become covered with bits of excavated materials (mineral or vegetable) and fragments of hyphæ, a considerable portion of which are swept into the infrabuccal sac. Similarly, in excavating cavities in decaying stems or roots, and in malaxating sound or moribund plant tissues, the workers produce a finely divided vegetable débris—containing more or less numerous fragments of hyphæ—much of which is scraped into the infrabuccal chambers of the imagines.

THE FUNGIVOROUS HABIT AMONG FORMICIDÆ

The data presented in this paper reveal the fact that ants are closely associated with fungi, but they do not indicate that the Formicidæ, other than the Attii, are fungivorous.[1] The cropping of aerial hyphæ does not indicate necessarily that fungi are eaten by ants. Furthermore, the spores and fragments of mycelia, which occur so characteristically in the pellets of imagines, appear to be detritus, cleaned from the bodies and appendages of the ants, rather than food-residues. The more or less "pure cultures" of particular fungi in the ant-inhabited stems of *Cuviera* and *Plectronia,* the pseudobulbs of *Myrmecodia* and *Hydnophytum* and the carton nests of *Lasius fuliginosus* and *L. umbratus* cannot be considered to prove that the fungi are actually cultivated and eaten by the ants. Unless all fungi are equally resistant to continued cropping, and react similarly in the peculiar environmental conditions within the domatia, certain species are likely to become dominant. If a particular form does become dominant and grows actively, it will be likely to be transferred to new nests by the queens, since the infrabuccal sacs of imagines almost invariably contain more or less numerous fragments of hyphæ or spores.

ANTS AS ACTIVE AGENTS IN THE DISSEMINATION OF FUNGI

That ants play an important rôle in the dissemination of disease has been suggested by Darling (1913), Wheeler (1914) and Studhalter and Ruggles (1915). Wheeler states in his paper upon "Ants and bees as carriers of pathogenic microorganisms":

> "It would seem to be possible, therefore, for ants to spread disease germs in three different ways: first, by simply walking over or into human food, as Darling has shown; second, by dropping into it infected hypopharyngeal pellets, and third, by contaminating it with their germ-laden feces."

As shown upon preceding pages, there is a general tendency among ants to take spores, fragments of mycelia and bits of decaying plant tissue into their infrabuccal pocket. In this sac the fungi become mixed with food-residues and mineral and vegetable detritus, forming a pellet which is subsequently voided upon any convenient surface. The composition of the infrabuccal pellet suggests that it is a "culture" or potential source of infection. Furthermore, von Ihering (1898), Huber (1905) and more recently Bruch (1919) have demonstrated that the hyphæ and spores in the voided pellets of Attiine queens actually are viable and give rise to luxuriant growths of hyphæ. In view of these facts, it seems probable that the Formicidæ are active agents in the dissemination of many of the higher fungi, particularly in tropical regions where ants are so numerous and ubiquitous.

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[1] The pellets in the trophothylaces of Pseudomyrmine larvæ contain spores and fragments of hyphæ and a variety of miscellaneous substances, but we have been unable to determine how much of this material is actually eaten by the larvæ.

ORIGIN OF THE FUNGUS-GROWING AND FUNGUS-FEEDING HABITS

There has been considerable speculation in regard to the origin of the highly specialized Attiine ants and of their remarkable fungus-growing and fungus-feeding habits. Von Ihering (1894) is of the opinion that the fungus-growing and leaf-cutting habits may have originated as a specialization from the seed-storing habit. Emery (1899) believes that the cropping of adventitious growths of hyphæ upon the walls of the domatia, "est vraisemblablement l'origine de la mycophagie exclusive des Attinæ." FOREL (1902) considers that in the early stages of the development of the biocoenose, the fungus-gardens were grown upon insect excrement, and Wheeler (1907) cites the habits of fungicolous termites and ambrosia-beetles in support of this hypothesis. The latter investigator states: "the method employed by the *Atta* queens in manuring their incipient fungus-gardens suggests that the food plant may have been originally grown on fecal substances."

There are certain general tendencies in the relations between ants and fungi which are worth mentioning in this connection. Thus, there is a general tendency for queens, as for other imagines, to transport spores and fragments of hyphæ in their infrabuccal cavity. This is of interest in discussing the extraordinary habits of the Attiine queens. Furthermore, I have called attention to the fact that there are more or less "pure cultures" of adventitious fungi in the nests of certain ants, which grow with particular luxuriance in those regions of the domatia where the detritus (pellets, feces, etc.) of the colony is deposited. If such mats of aerial hyphæ were edible, it would be a simple matter for the ants to increase the volume of their primitive fungus-gardens by adding extraneous materials, *i.e.*, insect excrement, vegetable débris, etc., to the original compost.

In conclusion, it is to be emphasized that my observations are based upon the study of specimens preserved in alcohol and, therefore, will have to be verified by experimentation with living organisms. However, they reveal a very general and close association between ants and fungi, and emphasize the necessity for further and more detailed investigations upon the structure and feeding habits of Formicidæ and the rôle of these insects in the dissemination of plant diseases.

The ants used in this investigation were obtained from the extensive collections of my colleague, Professor W. M. Wheeler, and have been carefully identified by him.

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DESCRIPTION OF PLATES

Plate VI

Fig. 1. *Cuviera species.* Section of "fungus-garden" and medullary substratum. × 160.

Fig. 2. Portion of infrabuccal pellet of *Crematogaster impressiceps* var. *frontalis.* This pellet was composed entirely of the ambrosia-like fungus. × 400.

Fig. 3. *Cuviera angolensis.* Section of the wall of a recently occupied myrmecodomatium, showing aerial hyphæ. × 210.

Fig. 4. Portion of an infrabuccal pellet of *Pachysima aethiops,* showing aerial hyphæ, spores and other detritus. × 330.

Fig. 5. Portion of a larval pellet of *Pachysima aethiops.* Spores resting upon a ground mass of coccid tissue. × 180.

Fig. 6. Portion of a larval pellet of *Pseudomyrma gracilis* (var. nov.), showing pollen and fragments of insect. × 58.

Plate VII

Fig. 7. Portion of an infrabuccal pellet of *Pseudomyrma gracilis* var. *mexicana,* showing pollen and various types of spores. × 330.

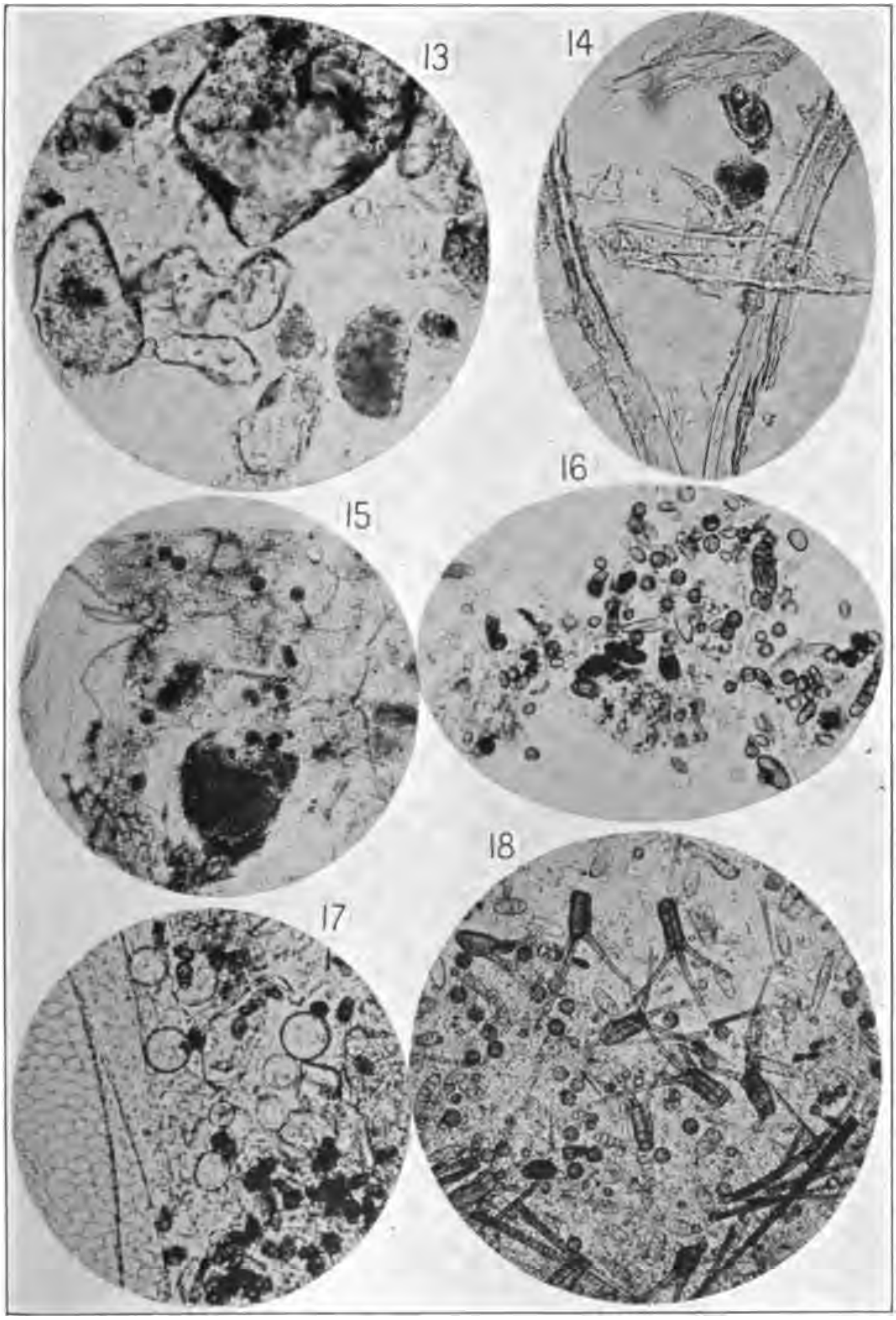
Fig. 8. Portion of an infrabuccal pellet of *Pseudomyrma decipiens.* This pellet was composed entirely of small, light colored spores. × 330.

Fig. 9. Portion of a larval pellet of *Pseudomyrma flavidula,* showing mixture of soft insect tissue and spores of various types. × 78.

Fig. 10. Portion of an infrabuccal pellet of *Pseudomyrma flavidula,* showing numerous hyphæ. × 330.

Fig. 11. Portion of an infrabuccal pellet of *Pseudomyrma flavidula* var. *delicatula,* showing various types of spores. × 330.

Fig. 12. Portion of an infrabuccal pellet of *Atta cephalotes,* showing vegetable débris and dirt. × 205.



Bailey on Ants and Fungi.

PLATE VIII

FIG. 13. Portion of an infrabuccal pellet of *Pogonomyrmex barbatus* var. *marfensis*, showing sand. × 322.

FIG. 14. Portion of an infrabuccal pellet of *Camponotus herculeanus* subsp. *ligniperda* var. *novaboracensis*. This pellet was composed entirely of the shredded wood of *Thuja occidentalis*. × 205.

FIG. 15. Portion of an infrabuccal sac of *Camponotus brutus*, containing spores, hyphæ and bits of decaying plant tissue. × 105.

FIG. 16. Portion of an infrabuccal pellet of *Diacamma australe*. This pellet was composed largely of spores. × 390.

FIG. 17. Portion of an infrabuccal sac of *Camponotus abdominalis* var. *costaricensis*, containing numerous spores and pollen. Note texture of membranous sac on left. × 322.

FIG. 18. Portion of an infrabuccal pellet of *Odontomachus haematoda*, showing great numbers of spores of different types, hairs, and dirt. × 205.

AN OVERLOOK OF THE RELATIONS OF DUST TO HUMANITY

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In considering the relations of dust to humanity we must not disregard the floating dust of the air, which probably is not brought to the earth except by means other than its own gravity. The "other" means is condensation. The water vapor of the air condenses first on these minute dust particles; thereby our rainfall is gentle and even in character during the shower. Were it not for this feature of nature, every shower would be a terrific cloud burst. The floating dust up to a height of six or seven miles—for moisture does not extend materially higher than cirrus clouds—is one of earth's greatest blessings. If life existed without it, life would be vastly different from what it now is.

The shell of wind-blown dust, as distinguished from the floating dust, is rarely thicker than half a mile. In arid regions where vegetation does not anchor it, wind-blown dust is a mighty physiographic agent. Dust carried more than a thousand miles from the Desert of Gobi fills the channel of the Hoang River, "China's Sorrow," until the bed and banks of the river are higher than the surrounding land. The river cannot clean out its channel; therefore it must make a new one. Seventy-five years ago its waters were poured into the delta of the Yangtse. Then the river broke its banks near Kaifeng. When things were settled the flood joined the Pechili, more than three hundred miles distant. That was merely one instance; for the history of that part of China is a record of the sorrow of Han—all from a single cause—the dust of the Gobi—catastrophic and destructive, not constructive.

In the Plains of this country we have another illustration. The wind-blown dust is delivered in such measure to rivers of the Platte type—"a mile wide, an inch deep, with bottom on top"—that the whole effect is beneficent. Rock waste born of the mountains to the westward is transported, distributed, and levelled.[1] The process is rarely destructive; almost always it is constructive. Billions of tons of mineral matter are yearly taken from a region that is non-productive, and converted into soil which has the potentiality of nutrition and life. But it is dust—all dust.

Now there exists another consideration of wind-blown dust that is confined to thickly-peopled regions where practically all the wind-blown dust is picked up from public streets. A small proportion—pollen, leaf dust, foliage smut, the eggs of insects, and the wing scales of lepidoptera—is gathered from swarded areas. Pollen excepted, the dust of swarded areas is not a menace. At its worst it merely breeds fine crops of infusoria when exposed in water. But wind-swept street dust is a menace to health, perhaps as dangerous as contaminated water.

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[1] The carrying power of the wind varies with the velocity. Double the velocity and the carrying power is increased 64-fold.

Let us assume that finely ground paving substance is the chief part of street dust. If the paving is a rock or brick surface the mineral matter—usually silicious—is sharp edged; therefore it cuts the soft tissues in which it lodges. Particles materially less than 2 micromillimeters in dimension are usually too small to become entangled in lung tissue; particles more than 3 or 4 micromillimeters in size are too large. Therefore size is an important factor. This statement cannot be taken too seriously, however, for it has exceptions.

The character of the dust of public streets is an important factor, and the dust is composed of whatever is dropped there. From the moment when anything reaches the street surface the grinding process begins. The rattan broom of the sweeper is the last instrument in the grinding process; and the process is completed when the cartman tosses the accumulation into the air with his shovel.

Next to paving material, horse dung is the most noteworthy component of wind-blown dust, and its lightest part, the fibrous cellular tissue, is not wholly freed from the soluble biliary part by the action of rain and street sprinkling; it retains a part of the soluble matter and also a rich content of germ life—bacilli, micrococci, and myxobacteria. Among the varieties of germ life most important in ecological science are the bacilli of tetanus and of tuberculosis. Cases of infection by the latter have been reported many times. Cases due to the first-named are rare unless they occur in connection with lacerations. The soil seems to be the home of the tetanus bacillus. A war scare made infected court-plaster, peddled by alleged enemy agents, a premeditated scheme for infection of communities. In evidence cultures of the suspected court-plaster produced tetanus bacilli. So also would anything else soiled by dirty hands. As a matter of fact, for every bacillus found on dirty court-plaster a myriad might be found on the handle of a garden tool, or on the hands of any youngster who plays marbles on the ground. The presence of tubercle bacilli in dust cannot be doubted but the danger from infection from the tubercle bacilli of street dust is slight as compared with the danger from the dust of a room occupied by a tuberculous patient. Nevertheless, dried sputum is a constituent of the street dust of cities, and cases of infection by means of it have been established beyond reasonable doubt. As a matter of fact tubercle bacilli are rarely absent from street dust, and in city streets they are generally the most notable feature of germ life.

The colon bacillus is almost always in evidence in street dust. It is a product of the horse dung content of such dust. The colon bacillus in street dust need not be a cause for alarm *per se*. When found in drinking water, however, there may be danger from the possible presence of typhoid bacilli, because both are characteristic of the enteric tract. As a rule, for every colon bacillus found in a glass of water, about a million find lodgment on articles of food exposed for sale on open street stands. Other forms of germ life a-plenty are constituents of wind-blown street dust but, so far as known, they play merely an insignificant part in the economics of humanity. They need not be considered here.

The foregoing paragraphs present a broad but very elementary view of the ecology of dust. So far as the floating dust of the atmosphere is concerned it is as necessary to life as watery vapor. From a meteorological standpoint the two cannot be considered separately. To assume that either is " foreign matter of the air " is infantile. If the oxygen and nitrogen were removed, the water vapor and dust motes would have the same general movements as the atmosphere as it now is constituted. The only material difference would be that condensation of the water vapor would carry some of the dust particles to the ground. When the water again became a vapor, electrification of the dust particles would project them into the air once more.

Wind-blown dust, however, may be considered very properly as " foreign matter of the air." Wind-blown street dust is disease-bearing. It can be taken out of the air, it is true; so also one may use a 40-ton truck to carry a postage stamp across the street. The real problem is to prevent street dust from getting into the air; and this is not difficult. If hard-paved streets are washed, the water carries to the sewer the dust which brooms cannot gather; and if macadamized and dirt streets are tarred, the dust will not fly from them. Within natural limits a community may have sanitary conditions that are beyond reproach. A community gets the sanitary administration it deserves, however, but not necessarily the one which it needs.

[Another article by Dr. Pedway giving further details of the dust of the Gobi desert will be published in a later number of Ecology.—EDITOR.]

SOME ECOLOGICAL ASPECTS OF THE TIDAL ZONE OF THE NORTH CAROLINA COAST

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The tidal zone of the North Carolina coast presents a wealth of ecological problems. This zone includes the narrow strip along the ocean front, sounds, and rivers, between the high and low tide levels. In this paper, however, the term tidal zone is restricted to the inner belt along the sounds and rivers not affected by the action of the waves of the ocean. The term strand is used for the zone of the beach exposed not only to the rise and fall of the tide but to the direct action of the waves of the sea and the sand blast. Ecologically these two regions are very different. The strand on our coast is practically bare of vegetation and frequented very largely by animals which are scavengers or beach combers. The tidal zone, on the other hand, is often an area of considerable extent and is usually well covered by grasses. At least three species of grasses grow luxuriantly here, a fine short grass growing principally about low tide level, a coarser grass growing principally in the pockets at higher level, and a fine matted grass growing near the high tide level. To these three should be added the common sea oats (*Uniola paniculata*) which starts just below high tide level and continues up into the higher dunes, and the salt marsh sedges which grow in shallow water and are more or less exposed at low tide. In addition to the areas covered by grasses there are many of considerable extent which are devoid of vegetation. The tidal zone supports a number of terrestrial forms which invade it during low tide, as well as several forms which live permanently here. We need look for no special adaptations in the former group as they are for the most part active creatures which make the most of any situation. In the latter class there are, however, many unsolved questions of interest, not the least important one being the factors which make it possible for these normally terrestrial air breathing animals to maintain themselves in a locality which is strictly aquatic for a longer or shorter period each day. Are we to look for morphological or for physiological adaptations? Are the groups that are present represented by a single species of several species? If a group is represented by several species, are the species of independent origin or are they perhaps descendants of an early ancestral type that has wandered into this region? These and many other questions might be asked. Some of them I believe can be answered even with the limited data at hand; others will require much more study.

A brief review of some of the papers bearing on the subject may help to make the problem clearer. Arndt (1) gives a short discussion of the results of this work in the between tide zone at Woods Hole, and lists seven species of terrestrial animals which occur there. Taxonomically these are distributed as follows: three insects of the order Homoptera, one of the order Heteroptera, and three spiders.

In regard to the insects Arndt (1) concludes that the three species of leaf hoppers are distributed in three zones, a lower zone of *Megamelus marginata,* a middle zone inhabited by a delphacid (species not determined), and an upper zone inhabited by a species for which the family is not even indicated. He also observes that the calcar on the *Megamelus* is large, that on the delphacid only intermediate in size, while the third species is without a calcar. He concludes from this that the calcar is an organ developed by the *Megamelus* to enable it to walk or leap about on the water; while the delphacid would have less occasion to walk on the water and hence a smaller calcar, and the leaf hopper, living in the higher regions not much subjected to inundations, is freed from this necessity and has no calcar. The absurdity of this position has been pointed out recently by Metcalf and Osborn (2), so that it is only necessary to note in passing that the calcar is a very specialized structure in a single subfamily of the plant hoppers (Fulgoridæ), and that it is as well developed in species occurring in arid situations as in species living either in the between tide zone or in swamps. Furthermore, Metcalf and Osborn have found *Deltocephalus marinus,* a species of Cicadellidæ without a calcar, living in short grass at the very edge of the water at low tide where it must have been submerged under from 8–10 feet of water at high tide. The paper just mentioned lists ten species of Homoptera belonging to eight genera distributed among six subfamilies of three families which occur in the between tide zone, and gives a discussion of the general ecological situation which surrounds these species. Other papers deal with species of animals living in the between tide zones, but so far as I am aware none deal with the modifications, either morphological, physiological, or ecological, that the species of this zone must undergo to enable them to maintain themselves.

The following incomplete notes are offered at this time in the hope of stimulating others to make observations in this interesting field.

So far as I am aware no vertebrates make their permanent home in the tidal zone region along our coast. Further south, in Florida, the beach mouse (*Peromyscus polionotus neverventris*) lives "on the sand dunes and beaches wherever there is a growth of sea oats (*Uniola*) which appears to be its principal food plant. It is a nocturnal animal and its nightly activities may be read early in the morning from the multitude of tiny tracks which lead in all directions and often form a network on the sand. A single track sometimes extends for a hundred yards or more from a burrow, and with all its windings may aggregate several hundred yards of travel, showing the activity of this small worker during many hours.

"Tracks are most plentiful immediately about growths of sea oats, patches of saw palmetto or scrubby bushes. The homes of these mice are usually in short burrows sheltered by growing vegetation or under fallen palm fronds. As in the case of many of our mammals we have scanty information concerning the life of these active animals" (3).

This mouse has not been collected in North Carolina, but may live in the abundant sea oats just at the edge of the tidal zone along our coast.

Birds of various species, especially shore birds, visit the tidal zone during migrations; but their connection with this zone is so limited that they cannot be said to be an important factor in its life.

The diamond-backed terrapin is a rare incidental visitor in which our interest is more gastronomical than ecological.

Arndt discusses three species of spiders belonging to the genera *Clubiona, Grammonata,* and *Lycosa.* Spiders of at least two species have been observed on our coast, but none have been identified.

Solitary wasps are also common on the sandy stretches of bare beach, and Kellogg (4) describes the behavior of a species of *Ammophila* on the salt marshes of San Francisco Bay. Another group of solitary wasps common on the strand and in the tidal zone is the velvet ants or cow killers (Mutillidæ). Since practically nothing is known about the life history or habits of these wasps nothing more can be done than to indicate that here is a profitable field of investigation.

The beach tiger beetle (*Cicindela dorsalis media*) is very common along the strand, and wanders up into the higher dunes. Although it is frequently taken in the tidal zone I have no evidence that it breeds there and hence must class it is an incidental visitor only.

The salt marsh cicada (*Tibicen viridifascia* Walk.) is common in the tidal zone along our coast, as has been recently pointed out (5). It must pass most of its life cycle either in close proximity to or within the tidal zone, as it breeds in the sea oats and, while the sea oats grows more abundantly above high tide level, some of it grows just at the border of high tide and would be inundated in case of storm or during times of especially high water. While the adults are active flying insects and could readily escape from the incoming tide the larvæ are subterranean and must be subjected to submergence at times.

Four species of Delphacids have been captured in this region, and, although they are active insects, some of them at least occur in such situations that it would seem impossible to escape the incoming tide. It is interesting to note that one of these species, *Megamelanus spartini* Osb., collected from sea oats, is described from the region of Cold Spring Harbor, Long Island, where it was collected from the common salt meadow grass (*Spartina patens*), which grows in situations similar to these in which we find sea oats along our coast. This species is restricted, therefore, to a habitat rather than to a food plant, and it is interesting to speculate on the forces that have brought about these conditions. It is easier for me to believe that these terrestrial animals have followed their mesophytic hosts into these half hydrophytic situations, and that their evolution has paralleled the evolution of their hosts; so that gradually these air-breathing animals have become adapted to a condition that is aquatic for part of the time. If this assumption is sound we have in this instance a species that has become adapted to a given locality and that has followed that locality regardless of food plants. So far as we have been able to discover these species show no morphological modifications that would fit them for long periods of submergence. What then are the physiological modifications that make it possible for these highly active terrestrial animals to remain inactive for long periods of submergence?

Three other species of plant hoppers (Fulgoridæ) have also been taken in this region, but, since they have been reported on elsewhere (2), no discussion is required here.

Two species of leaf hoppers (Cicadellidæ) occur on grasses growing rather close to low tide level, and, since the nymphs of both species have also been taken in the same situation, it seems safe to conclude that they are naturally confined to this zone. While they both belong to the same genus, *Deltocephalus,* this genus is such an extensive one, and the species are so different in many of their characters, that it hardly seems probable that they are descendants of a common ancestor living within the tidal zone but rather that they have had an independent origin outside of this zone.

The beach grasshopper (*Trimerotiopis maritima*), like the beach tiger beetle, really belongs to the strand and higher sand dunes, and, while it is too active an insect to be caught by the incoming tide, it wanders into the tidal zone so commonly that it must be mentioned here.

Three species of fiddler crabs occur along our coast, and, while all three of them occur in the tidal zone, *Gelasimus pugelator* occurs more commonly on our sandy beaches, especially at tide level where the beach is fringed by sedges and grasses. Countless numbers occur on our beaches, and a belt averaging a foot or more in width and extending for several miles is not uncommon. *Gelasimus pugnax* occurs more commonly along rivers where it haunts the boggy marshes that are exposed at low tide (6). *Gelasimus minax* seems to prefer the higher banks and dunes where it lives a more or less solitary life. It is exceedingly active, and, while rarer along our coast in comparison with the other two species, still it feeds on the tidal zone at low tide, and the females go down to the edge of the water to lay their eggs, so that its life is more or less intimately connected with the tidal zone.

Numerous snails feed on the sedge exposed at low tide, and are so abundant that in favorable localities it is rather the exception to find a sedge that does not support one or more.

In such a general discussion one can hope to merely open the field for consideration, and to direct attention to the possibilities and many unsolved question involved.

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THE LIMESTONE PRAIRIES OF WILCOX COUNTY, ALABAMA

ROLAND M. HARPER

Wilcox County lies just south of the well-known black prairie belt of Alabama, and all available statistics of soils, vegetation, population and agriculture point to its being the most fertile county south of that belt. Much of its fertility is due to the presence of several square miles of strongly calcareous soils in the northeastern half. A strip averaging four or five miles wide at the inland edge of the county is characterized by the Ripley formation (uppermost Cretaceous), which has considerable limestone and marl in it, and east of the Alabama River this is bordered on the south by the Midway limestone, of lowest Eocene age. The superficial non-calcareous clays and sands (commonly, or at least formerly, referred to the Lafayette formation) which cover much of the surface of the coastal plain farther south and east are very limited in extent in Wilcox County, so that most of its soils are residual from the Cretaceous and Eocene strata.

In Dr. Eugene A. Smith's report on the coastal plain of Alabama, published by the state geological survey early in 1895 (pp. 194, 591, 592), the "cedar brakes" on that phase of the Midway formation called by him the "Nautilus rock" (from one of its characteristic fossils) in the eastern part of Wilcox County are briefly described. In the soil survey of this county by R. A. Winston and N. E. Bell, published by the U. S. Bureau of Soils in March, 1918, the limestone soils are located for the first time on a map. Four types of distinctly calcareous soils are described in the soil survey report, aggregating 35,264 acres or a little more than six percent of the area of the county. In order of extent they are "Sumter clay," "Houston clay," "Trinity clay," and "Houston fine sandy loam."[1] It happens that practically none of these are visible from any of the railroads traversing the county, and I never saw any of them until I made a special trip on foot for the purpose, across country from Greenville to Snow Hill on June 11–12, 1919.

S. B. Buckley, a botanist and geologist who taught school for a few years around 1840 at Allenton, within a few miles of the largest areas of limestone outcrop in Wilcox County, must have been familiar with them, but in his day such a thing as describing vegetation was scarcely thought of, so that we can judge of his explorations only by the localities given for plants collected by him. In the American Journal of Science **45**: 170–177, 1843, he described several supposed new species, among them *Phacelia pusilla* (now regarded as synonymous with *P. dubia*), from "Prairies of Alabama," without definite locality, but since credited to Wilcox County by Mohr. In the Proceedings of the Academy of Natural Sciences of Philadelphia for 1860, pp. 443–445, he described two trees from Wilcox County, but without precise localities. In Mohr's Plant Life of Alabama (1901) I have found 39 species cited as having been collected by Buckley, all but six in Wilcox County; and most of them are characteristic of calcareous soils, though not of prairies. (There seems to be nothing in Dr. Mohr's book, by the way, to indicate that he ever explored Wilcox County himself.)

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[1] The first two series names are misnomers, for these soils are quite different from anything in Sumter County, Georgia, or near Houston, Texas.

It appears from the descriptions in the two works first mentioned that the principal cedar-brake area in the county is the "Houston fine sandy loam," which is nearly all in one body about six square miles in extent, a few miles southeast of Snow Hill. (This is derived from the Eocene "Nautilus rock," while the other three calcareous soil types are mapped as occurring in both the Cretaceous and Eocene parts of the county.[2]) Accordingly ingly I directed my steps thither. Before reaching the fine sandy loam I passed over about two miles of "Sumter clay," a rolling country with drab-colored sticky clay soil, almost uninhabited on account of the scarcity of good water, but nearly all cultivated at one time or another. Like the calcareous parts of the black prairie belt to the northward, this area is now covered mostly with such weeds as *Melilotus alba, Monarda citriodora,* and *Erigeron ramosus,* which are used for hay and pasture.[2a] Along fence-rows and water-ways are such trees as *Juniperus Virginiana, Celtis occidentalis* (?), *Quercus Muhlenbergii, Populus deltoides,* and *Diospyros.*

The "Houston fine sandy loam" area has the limestone rock near the surface, and the soil is somewhat sandy, as the name implies, the sand being doubtless derived from sandy layers in the limestone, and not from any later superficial formation. Where the soil is deep enough it has been cultivated in times past and is now devoted mostly to hay and pasture, like the "Sumter clay." But considerable areas have the rock coming right to the surface, making plowing impossible, and in such places is found some natural prairie vegetation. Throughout the area of that soil the cedar, *Juniperus Virginana,* is practically the only tree. The herbaceous vegetation is very interesting. As in many other places where the soil is very thin, and where there is more rain in spring than in summer, there are quite a number of annuals which bloom in spring and wither away before summer, and no doubt there are also some autumnal species hardly recognizable in June, so that it would be necessary to visit the place at more than one season to get a complete list of the plants.

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[2] In the discussion of the "Sumter clay" in the soil report it is stated that "The soil is derived from the weathering of Cretaceous limestone"; but that is true of only about two-thirds of it in Wilcox County (and of no soil in Sumter County, Georgia, where that series name was first applied).

[2a] See fig. 2, page 27, "Resources of Southern Alabama," Sp. Rep. 11, Geol. Survey of Ala., 1920.

The commonest species in the areas of natural prairie, in order of abundance, as nearly as I could determine in one forenoon, are as follows:

Andropogon scoparius
Polygala grandiflora
Fimbristylis puberula
Houstonia angustifolia
Prunella vulgaris
Erigeron ramosus
Verbena angustifolia
Gaura angustifolia?
Sabbatia angularis
Cyperus ovularis?
Coreopsis auriculata?
Mesadenia tuberosa
Polygala Boykinii
Rudbeckia triloba
Opuntia vulgaris?
Arenaria patula
Sisyrinchium sp.
Ambrosia artemisiifolia
Lepidium Virginicum
Specularia perfoliata
Galactia sp.
Lespedeza sp.

There was also an unidentified moss in some of the more open and rocky places. The first herb listed was by far the most abundant of all. (See fig. 1.)

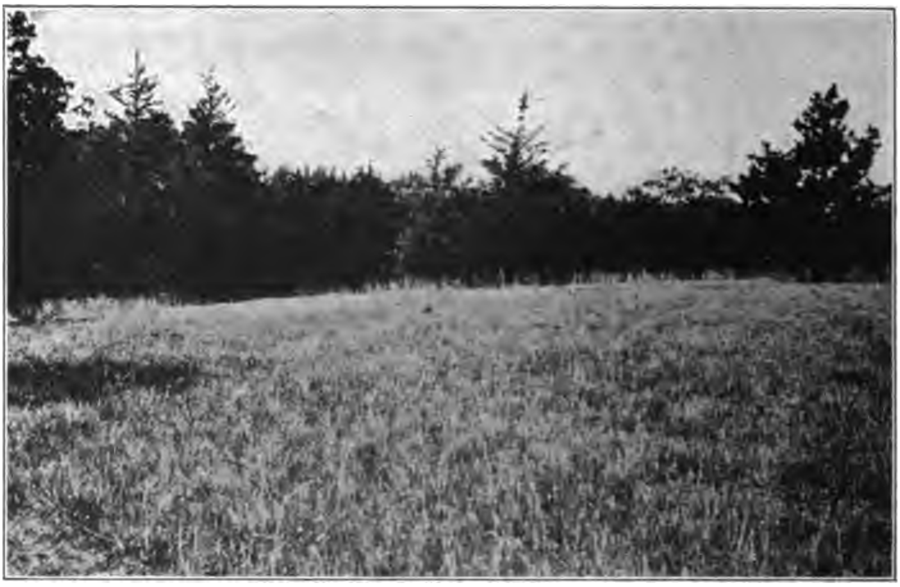

FIG. 1. Natural prairie vegetation on "Houston fine sandy loam," where the limestone comes to the surface. The most conspicuous herb is *Andropogon scoparius*, and the trees are mostly *Juniperus Virginiana*.

A few of the less abundant species are weeds, probably introduced through the agency of cattle, but the majority are unquestionably native. This vegetation bears considerable resemblance to that of some chalk outcrops or bald prairies in the black belt, described by Mohr (Plant Life of Ala., p. 104), and probably has some features in common with the limestone barrens or cedar glades of Middle Tennessee, which have been mentioned several times in the writings of Gattinger and others, but apparently never yet described by a plant sociologist or student of vegetation.[3] But the occurrence of such plants as *Andropogon scoparius, Fimbristylis puberula* and *Polygala grandiflora,* which grow more commonly in poor sandy soils, seems rather paradoxical. One explanation suggests itself, however. Where the rock comes to the surface or near it earthworms must be absent or practically so (as they seem to be in most sandy soils, and on the Hempstead Plains of Long Island, for a different reason[4]), and it is very likely that these plants, like the Ericaceae, many orchids, etc., cannot tolerate the presence of worms about their roots. The omnipresent cedar, too, seems to be a helminthophobe (if one may coin such a term), as I have suggested elsewhere.[5]

The cedar indicates also another feature of the environment that is exceptional in prairies, namely, the rarity of fire.[6] *Houstonia angustifolia* seems to be another pyrophobe, growing both in dry sand and on limestone outcrops, but apparently always in places pretty well protected from fire. These limestone prairies therefore differ radically from the well-known prairies of Illinois, which are said to be well supplied with earthworms, and were noted for prairie fires before they were reduced to small isolated areas by the settling up of the country; and there is apparently not a single native species common to the two areas. Just why fire should be so rare in this part of Alabama it is hard to say, unless it is because of the small size of the individual prairies,[7] those I saw covering only a few acres each.

Just before passing out of the limestone area (whose northwestern boundary is pretty sharp) I examined a small densely wooded valley whose vegetation is worth putting on record here, to illustrate the effect of strongly calcareous soils and abundant humus in that climate (see fig. 2). The commonest species there seemed to be as follows:

Large Trees

Quercus Muhlenbergii
Fraxinus Americana
Juniperus Virginiana
Juglans nigra
Ulmus alata
Liquidambar Styraciflua
Quercus Schneckii
Tilia sp.
Liriodendron Tulipifera
Quercus stellata

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[3] For references to several incomplete descriptions of the Middle Tennessee cedar glades see Torreya, 12: 154. July, 1912.

[4] See Mem. Torrey Bot. Club, 17: 267. June, 1918.

[5] Torreya, 17: 141. Aug., 1917.

[6] See Torreya, 12: 147. July, 1912.

[7] See Plant World, 20: 60. 1917.

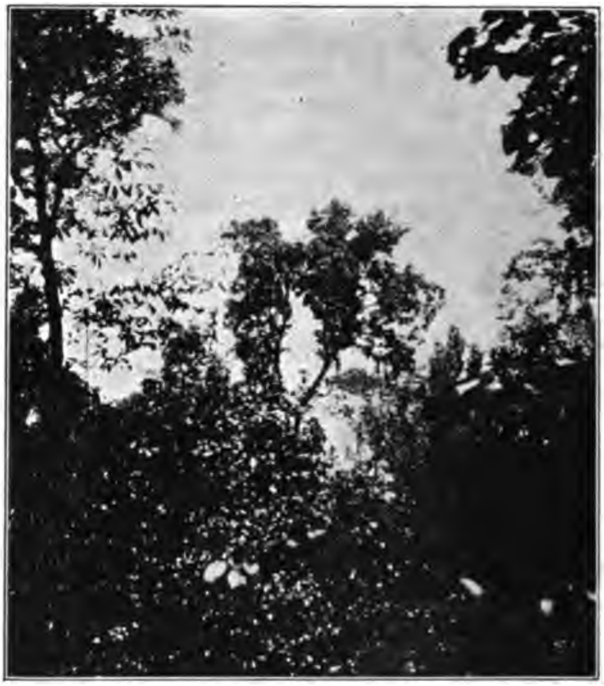

FIG. 2. View in rich woods in limestone valley, showing *Quercus Muhlenbergii, Juglans nigra, Fraxinus Americana, Tilia,* etc.

SMALL TREES

Cercis Canadensis
Prunus Americana
Ostrya Virginiana
Viburnum rufidulum

SHRUBS AND VINES

Rhamnus Caroliniana
Berchemia scandens
Callicarpa Americana
Vitis aestivalis
Rhus radicans
Parthenocissus quinquefolia
Cornus stricta?
Bignonia crucigera

HERBS

Tillandsia usneoides
Uniola laxa
Polypodium polypodioides
Elephantopus tomentosus
Sanicula gregaria?
Arisaema Dracontium
Smilax herbacea
Ruellia strepens?
Dodecatheon sp.
Rudbeckia triloba?
Geum Canadense
Erythrina herbacea
Onosmodium sp.

The first and third herbs are epiphytes, and therefore not directly connected with the calcareous soil, though they undoubtedly obtain considerable inorganic nutriment from the decay of the bark on which they grow, instead of getting all their food from the air and rain, as might be supposed.[8] The rest are practically all "mesophytes," but it is not safe to assume that they are all calciphiles. For, as I have pointed out elsewhere,[9] many supposed lime-loving plants are really potash-loving, and can be found also in soils well supplied with potassium but not markedly calcareous. Potassium is essential to most plants, but calcium is less so, and may even have a dwarfing effect in some cases.[10] The luxuriance of vegetation in many limestone areas is probably due to the fact that limestone dissolves more rapidly than most other rocks, thus liberating whatever plant foods may be mixed or combined with it.[11] Snails, earthworms, and other humus-building animals also thrive on a calcareous diet, and thus expedite the formation of humus in limestone regions, where it is not prevented by fire, evaporation, erosion, or something of the sort.

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[8] See Am. Fern Journal, 9: 99–103. Jan., 1920.

[9] Bull. Torrey Bot. Club, 40: 396–399. Aug., 1913.

[10] In this connection see Gile and Ageton, Porto Rico Exp. Sta. Bull. 16 (the effect of strongly calcareous soils on the growth and ash composition of certain plants). 1914; Cowles, Bot. Gaz., 59: 163, 1915. (Review of a paper on the influence of lime on vegetation in Siam.)

[11] Fernald, in his well-known paper on the soil preferences of certain alpine and subalpine plants (Rhodora, 9: 149–193. 1907; reviewed by Cowles in Bot. Gaz., 45: 138–139, and by Hilgard in Science, II. 27: 140–143) has pointed out the marked floristic contrast between potassic, calcareous and magnesian rocks in northern New England and farther north. The plants said to be characteristic of potassic rocks (granite, etc.) are largely Ericaceae and other "oxylophytes," from which a hasty reader might infer that potassium has little effect on vegetation. But the potassic rocks mentioned by Fernald are hard and decompose very slowly, so that they yield their soluble constituents to vegetation at a far slower rate than would a soil of the same composition, or a limestone containing considerably less potassium.

In G. P. Merrill's "Rocks, Rock Weathering and Soils" (revised edition of 1906), pp. 185–226, are numerous analyses of rocks from various places in both hemispheres, and the soils derived therefrom, from which it appears that in the case of granite and other crystalline rocks the percentage of potash and soda is nearly always much less in the soil than in the rock, while in the case of limestone the percentage of the alkali metals increases with weathering. In a limestone from northwestern Arkansas the percentage of potash (K_2O) was 0.35 in the rock and 0.96 in the residual clay derived from it, and in one from the Shenandoah Valley of Virginia the potash increased from 1.08 percent to 4.91 percent with weathering.

PLANTS AND ANIMALS OF MOUNT MARCY, NEW YORK, PART II

Charles C. Adams, George P. Burns, T. L. Hankinson, Barrington Moore, and Norman Taylor

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IV. Plants and Animals

Part I of this paper, published in Vol. 1, No. 2, of Ecology, contained a general account of the topography, geology and climate of Mount Marcy, the general features of the plants and animals, and the instrumental data on the local environment of the habitats studied, but the details and ecological relationship of each was left for Part II.

There are certain definite types of vegetation, corresponding with definite habitats, in which the instrumental stations were placed. A description of what plants and animals live in these habitats is here presented, not only as a record and to be correlated with our instrumental data, but to trace as far as possible the history of the mountain biota and intermingling of species.

The Fir Forest.—The forest is practically continuous except for two openings of much ecological significance, the bog at Lake Tear, which is a depression, and the alpine summit, an elevation.

The belt of forest considered in this study is that growing between 4,250 and 4,900 feet in elevation, its lower limit distinguished by the disappearance of red spruce, *Picea rubens,* and its upper limit by timber line. It may be considered as a single vegetative unit composed of almost pure fir, *Abies balsamea,* with only a small admixture of paper birch, *Betula papyrifera,* but there is a marked difference in the height and diameter of the trees. At 4,250 feet the average mature firs approximate 40 to 45 feet by 8 to 10 inches in diameter at breast height; at timber line they do not exceed 7 to 12 feet in height by 5 inches (average about 3) in diameter. The change is not uniform, and stunting not very noticeable below elevations of about 4,500 feet. The stand is more nearly even-aged than would be expected with fir, and is on the whole mature. Younger trees are, however, found throughout. Reproduction is abundant in all the openings.

The value of this forest is for watershed protection, and scientific and scenic interest. Although trees large enough to be merchantable occur up to about 4,500 to 4,600 feet, the steepness and roughness of the slopes would make exploitation difficult and probably unprofitable.

LOWER LIMIT OF FIR FOREST.—The point selected for this station is about half way from the place marked *Camp* (it is only a camping site) on the topographic sheet, on the trail from Upper Ausable Lake to the summit of Marcy, and the intersection of this trail with one leading to Mt. Skylight. At this place the grade is steep and the woods dense, so dense in fact that off the trail one has to cut one's way.

The forest at this point, which appears to be typical of thousands of acres with similar conditions, is composed of about 85 percent *Abies balsamea,* 10 percent *Betula papyrifera,* and 5 percent *Picea rubens.* Practically no deciduous shrubs are found as undergrowth, which is characterized by many young plants of the fir, a few of the birch, and a very small proportion of the spruce. Nearly all the trees at this point average approximately 40–45 feet high.

Under the dense shade of such woods the forest floor, nearly shrubless except in clearings, is a deep carpet of mosses, save where the moss gives way to a thick mat of needles and litter. The mosses are chiefly *Sphagnum acutifolium, Hypnum Schreberi, Dicranum scoparium* and *Dicranum longifolium.* On the higher parts of this moss carpet, on rocks and on tree stumps, is *Cladonia rangiferina,* a lichen so common that it adds a gray tone to the somber woods. This is still more true as one ascends to higher elevations.

The absence of tree reproduction as well as of herbs and shrubs under the dense coniferous canopy has been commonly attributed to lack of light. Unquestionably light is important, but is not the only factor, for the soil moisture is considerably less under a thick canopy than in small openings. This lower moisture content has been found, in some cases at least, to be even more important than lack of light.[17]

Upon the forest floor of mosses and lichens the dominant herb is *Cornus canadensis,* its scarlet berries very abundant on August 22. Next to it in frequency is easily *Solidago macrophylla,* in full flower at this time. These two plants often make up the almost exclusive growth in the shade of the trees, but scattered through them are other species, notably *Oxalis Acetosella,* which is often locally dominant.

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[17] Moore, Barrington, "Reproduction in the Coniferous Forests of Northern New England," Bot. Gaz., Vol. 64, No. 2, pp. 149–158, 1917 (see especially p. 156). Burns found in Northern Michigan that openings which were filled with young sugar maple (*Acer saccharum*) had more soil moisture as well as more light and more heat. He further found, in unpublished experiments made in a forest nursery in Vermont, that an abundant moisture supply counterbalanced the shade produced by six thicknesses of cheese-cloth. R. E. Horton (Mon. Weath. Rev. 47: 603–623, 1919, Science, 51: 439, 1920) found the interception of precipitation by trees to be "about 25 percent as an average constant rate for most trees in heavy rains of long duration." The average of 11 trees in the summer of 1918 was 40 percent.

Other plants in this forest, arranged in the order of their frequency are

Linnæa americana
Chiogenes hispidula
Coptis trifolia
Monotropa uniflora
Clintonia borealis
Carex intumescens
Vaccinium augustifolium
Viola (sp. no flowers or fruit)
Cinna latifolia
Aralia nudicaulis
Lycopodium annotinum
Rubus strigosus (in more open places)
Ribes glandulosum
Streptopus roseus
Dryopteris dilatata
Osmunda Claytoniana

In quite open places are occasional shrubs of *Amelanchier spicata,* about 3–4 feet high, but these are scarcely known from the deeper part of the woods.

While the upper limit of red spruce is the deciding characteristic of this area, the fact remains that there is here a curious welding of floral elements from above and below. No true alpine plants have come down from the top to this region, for there is scarcely one of the plants listed which could not be found in the upper level of the Catskills. Yet the shade, the very existence of the habitat which these woodland plants demand is provided by the fir which here makes up 85 percent of the forest. Down the mountain a little further this fir meets stronger competition of the red spruce, which becomes dominant still lower down. So far as the forest is concerned, the red spruce practically gives way at 4,250 feet to the fir. It is a good illustration of the herbs of moderate elevations (for the Adirondacks) running well ahead of their natural shade, the red spruce, through the mingling of spruce and fir, and up through the fir to the very edge of the timber line. Yet not one true alpine plant has penetrated down through the fir forest to this level.

The fir, which is found in protected places, almost to the summit of Marcy, hundreds of feet above timber line, successfully meets the competion of lower-elevation trees, showing an adaptability to diverse conditions immeasurably greater than its herbaceous associates on the summit which are unknown in these woods.

Conversely most of the plants associated with this upper limit of the spruce, denizens on the whole of lower elevations, seem perfectly at home at this level. Their frequency of occurrence is different at different elevations above this, but not many of those listed fail to reach the topmost limits of the forest. More will be said of this in the discussion of the forest-floor vegetation just below timber line, and of the vegetation above that point.

VERTEBRATES OF THE FIR FOREST.—For comparison with the fir forest of the higher altitudes the following brief summary of recorded observations on the mixed hardwood area are of special interest.

While passing along the stream bed between the Upper and the Lower Ausable Lakes, two Deer, *Odocoileus americanus borealis* Miller, were seen; one was a fawn about half-grown. It is likely that many species of birds are present in the lower forest. Eaton[18] (pp. 42–50) describes the bird life of the Marcy region as he noted it in the early part of the summer of 1905, and found over a hundred species of birds nesting within ten miles of the mountain (p. 50). Since, although the forest cover is continuous, less than 30 species of birds nest above the hardwood zone (2,500 feet), it is very probable that most of these species are practically confined to the mountain base and that this is the chief bird habitat of Mount Marcy.

Miller[19] records over thirty species of mammals from Essex County, New York, and most of these from the lowland areas, principally from Elizabethtown. Very probably most of these species live on Mount Marcy. Other birds were noted here, but these were not clearly enough seen for identification. Most of these were warblers.

Above the hardwoods in the fir forest a small flock of perhaps a dozen white-winged crossbills, *Loxia leucoptera,* flew to some tree tops near our camp. Red-breasted nuthatches, *Sitta canadensis,* were often heard. In Eaton's account (loc. cit., pp. 42–50) the following species were found on the upper part of Mount Marcy above 4,000 feet, and undoubtedly in the growth of tall balsams and red spruces: Arctic three-toed woodpecker, *Picoides arcticus,* three-toed woodpecker, *Picoides americanus americanus,* blue jay, *Cyanocitta cristata cristata,* Canada jay, *Perisoreus canadensis canadensis,* slate-colored junco, *Junco hyemalis hyemalis,* black and white warbler, *Mniotilta varia,* myrtle warbler, *Dendroica coronata,* pine warbler, *Dendroica vigorsi,* winter wren, *Nannus hiemalis hiemalis,* red-breasted nuthatch, *Sitta canadensis,* Acadian chickadee, *Penthestes hudsonitus littoralis,* golden-crown kinglet, *Regulus saprapa saprapa,* ruby-crowned kinglet, *Regulus calendula calendula,* Bicknell's thrush, *Hylocichla aliciæ bicknelli,* olive-backed thrush, *Hylocichla ustulata swainsoni,* hermit thrush, *Hylocichla guttata pallasi,* and robin, *Planesticus migratorius migratorius.*

Of these species the following were found by Eaton breeding on Marcy between altitudes of 3,900 feet and 4,300 feet: Three-toed woodpecker, winter wren, black and white warbler, olive-backed thrush, and hermit thrush. Undoubtedly a number of other species use the tall conifer zone for nesting, where one important condition at least, namely seclusion, can be readily found. On account of the density of the cover and the extensiveness of this balsam forest, little was learned of the birds and other vertebrates of the region in our limited time. Juncoes, golden-crowned kinglets, and myrtle warblers were abundant and prominent, and the notes of some of these birds were heard at almost all times during good weather about our camp, and along the trail near it.

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[18] Eaton, E. H., "Birds of New York," Memoir 12, Part 1, New York State Musepm, pp. 1–501, 1910.

[19] Miller, G. S., "Preliminary List of New York Mammals," Bull. N. Y. State Mus., Vol. 6, No. 29, pp. 271–390, 1899. See also "Key to Land Mammals of Northeastern North America," l. c., Vol. 8, No. 38, pp. 59–160, 1900.

During the few days of field work little evidence of mammal life was noted in the region of tall balsams. Some deer tracks were seen along the trail not far from camp, and we were told by guides that the region is frequented by many deer on account of its relative inaccessibility to hunters. A little trapping was done for small mammals in the woods near camp, with wooden mouse traps, baited with bacon and corn meal. A white-footed mouse, *Peromyscus maniculatus gracilis* (LeConte), and two red-backed mice, *Evotomys gapperi gapperi* (Vigors), were taken.

There are very few published records of mammals occurring in this high coniferous forest on Marcy. Colvin[20] (p. 366) reports tracks of a panther, *Felis couguar* Kerr, near Lake Tear, and from these tracks and those of varying hares he inferred that the panther was hunting hares. He also records martens, *Martes americana americana* (Turton), in forests on the side of Mount Marcy, but says they do not occur above the timber line. He notes that they also destroy hares. Tracks in snow made by a small shrew were noted by him; these he considered to be *"Sorex personatus,"* an inference which is probably correct, since Batchelder writes that the masked shrew, *Sorex personatus personatus* Geoffrey, is apparently common there and found anywhere on the mountain. Colvin also notes tracks of ermine, *Mustela noveboracensis noveboracensis* Emmons (p. 369), also fisher, *Martes pennanti pennanti* (Erxleben), and lynx, *Lynx canadensis canadensis* Kerr (p. 367). The later was near Lake Tear and also evidently hunting hares. He reports the common red squirrel (probably *Sciurus hudconicus loquax* Bangs) at 4,000 feet elevation feeding on seeds of spruce (p. 370), and he saw (p. 172) a bear, *Ursus americanus americanus* Pallas, near the headwaters of John's Brook, on the northeast side of Mount Marcy.

Mr. C. F. Batchelder in a letter writes of taking the red-backed mouse, *Evotomys gapperi gapperi* Vigors, masked shrew, *Sorex personatus personatus* Geoffrey, and rock vole, *Microtus chrotorrhinus chrotorrhinus* (Miller), in the tall conifer region on the upper part of Mount Marcy. The latter was probably taken here, but possibly in the region higher up.

A frog was heard about the grassy stream border near camp and a glimpse was had of it. Very probably it was *Rana pipiens* Gmelin. A toad, *Bufo lentiginosus americanus* (Holbrook) Cope, was taken along the trail at about 4,500 feet. No other amphibians or reptiles were seen, although special search was made, and at the time of observations weather conditions seemed favorable for these animals; but the short time of existence of these conditions (two or three months during the year) probably prevents amphibians living permanently at high altitudes on Mount Marcy. Warm-blooded vertebrates can withstand long periods of cold weather, and the dense forest cover here is undoubtedly a very favorable condition for giving them protection from enemies and from storms. There is food here for birds and mammals. Insects and seeds of conifers, and the seeds and fruits of the undergrowth are present. The following common plants here have fruits available for animals: *Abies balsamea, Cornus canandensis, Oxalis Acetosella, Unifolium canadense, Clintonia borealis, Amelanchier spicata, Potentilla tridentata* and *Trientalis americana.*

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[20] Colvin, V., "Seventh Annual Report of the Topographical Survey of the Adirondack Region of New York. to the Year 1879," Albany, 1880.

Bog at East End of Lake Tear, 4,320 Feet.—This lake of perhaps two acres is the chief source of the Hudson River, and the highest permanent body of water in the State (see fig. 5 in Part I). Its eastern end is bordered by a bog of about 10 acres in extent which, in heavy rains, is sometimes nearly drowned. The lake, sheltered from the wind, beautifully reflects the forest of fir which surrounds it on three sides. The steep evergreen-clothed slope of the surrounding terrain makes an admirable setting for this little mountain lake which has drawn cries of astonishment at its beauty from Colvin, Roosevelt and hosts of less renowned visitors. No aquatic flowering plants are found in the lake, the short growing season and the cold water probably preventing their establishment. On August 20 the water at 3 feet deep was 50.5° F.

The bog is not quite level and has a slow-moving, poorly draining stream flowing through it from the eastward toward the lake. This stream is irregular in its meanderings, of varying depth, and frequently is lost under the mass of bog plants that bridges over its course. Due to changes of level in the water, local irregularities of the surface, boulders that are covered by vegetation, and thus perched above the general water level, and to mounds that support trees, there are several different types of plants growing in the bog and they are associated in different ways.

In that part of the bog nearest the lake and to water level, perhaps an irregular band of 20–40 feet, the dominant plant, which makes a close mat or turf on *Sphagnum* is *Carex oligosperma,* a far northern species unknown in the Catskills, but here making dense growths. It was fruiting freely in the lower parts of the bog, only sparingly so on higher parts. Scattered through the sedge are a few plants of *Calamagrostis neglecta,* a grass not reported heretofore from New York State. It fruits very sparingly nearest the water level of the lake, but higher up in the bog numerous fruiting specimens were noted. With this grass are also scattered patches of *Carex interior,* a freely fruiting sedge found quite down to the water's edge. This turf-like growth of grasses and sedges which is often 8–12 inches high has a lower story of vegetation flat down on the *Sphagnum* and usually half hidden by the stems of the grasses and sedges. This ground-hugging element of vegetation is *Oxycoccus Oxycoccus* and *Andromeda polifolia,* never over 3–4 inches high. Very rarely are there plants of *Gentiana linearis,* elsewhere common on the upper reaches of Marcy. This lowest part of the bog is practically composed of two sedges, a grass, a cranberry and the wild rosemary. Only one of these plants, *Carex interior,* is known in any quantity from lower elevations. The other species, even if found at more moderate elevations, have all come from greater ones, and as we shall see, are common on top of Marcy, except *Andromeda polifolia.* So far as our records show, they are unknown between the level of Lake Tear and the timber line.

Perhaps three fifths of the total area of the bog, while practically level, is a few inches above that just described and contains somewhat different species of plants and quite different proportions of those common to both. Here again it is a turf-like growth but the dominant plant is *Calamagrostis neglecta* which fruits very freely. The sub-dominant plant is *Andromeda polifolia* while scattered through it and rather common, is *Gentiana linearis.* In isolated clumps are scattered plants of *Veratrum viride,* which is not infrequent. Less frequent and somewhat sporadic in their distribution are some low woody plants and a few herbs. Arranged in the order of their frequency they are:

Lonicera cærulea
Vaccinium uliginosum
Vaccinium cæspitosum
Chamædaphne calyculata
Oxycoccus Oxycoccus
Carex oligosperma (not in fruit here)
Potentilla tridentata
Houstonia cærulea
Ledum grœnlandicum
Coptis trifolia

Towards the upper or southeastern end of the bog are a few scattered trees of *Abies balsamea,* about ten in all. They are well separated from one another and from the fir forest along the edge of the bog, and are usually growing on mounds of *Sphagnum* a foot or two above the general level. Seedlings of the fir, where the general level is not too low, are common (fig. 15).

Besides these mounds which are crowned with firs, there are several without trees on them, usually scattered boulders now quite covered with vegetation which is well above the general water level of the bog. These mounds contain all the plants so far recorded from the bog, with the addition of *Chiogenes hispidula, Linnæa americana, Trientalis americana, Spiræa latifolia, Unifolium canadensis,* and *Drosera rotundifolia,* which is rare. On one such mound in the extreme northeastern corner of the bog, the rock is covered almost exclusively by *Empetrum nigrum* (fig. 15). The occurrence of this and a few other plants already noted in this bog, hundreds of feet below the bare summit of Marcy, which is in plain view, but separated by an unbroken fir forest, is interesting. It may well be that the occurrence of this crow-berry and of *Lonicera cœrulea, Vaccinium cæspitosum, Vaccinium uliginosum,* and *Calamagrostis neglecta,* in this bog at 4,320 feet is the lowest elevation from which they are known in the Adirondacks. Our records from other sides of Marcy show some of them only above the timber line which is at about 4,900 feet. All except the grass were found on Mt. McIntyre at 4,800 feet, but only rarely, usually growing at greater elevations, and nowhere below the timber line. This little island of alpine and subalpine plants, evidently in a locally favorable habitat, surrounded by a dense fir forest, apparently isolated, and at a considerably lower elevation than the ecologically related plants above the timber line, was the deciding factor in choosing this bog as one of the critical points in the response of the plants and animals of Marcy to their environment.

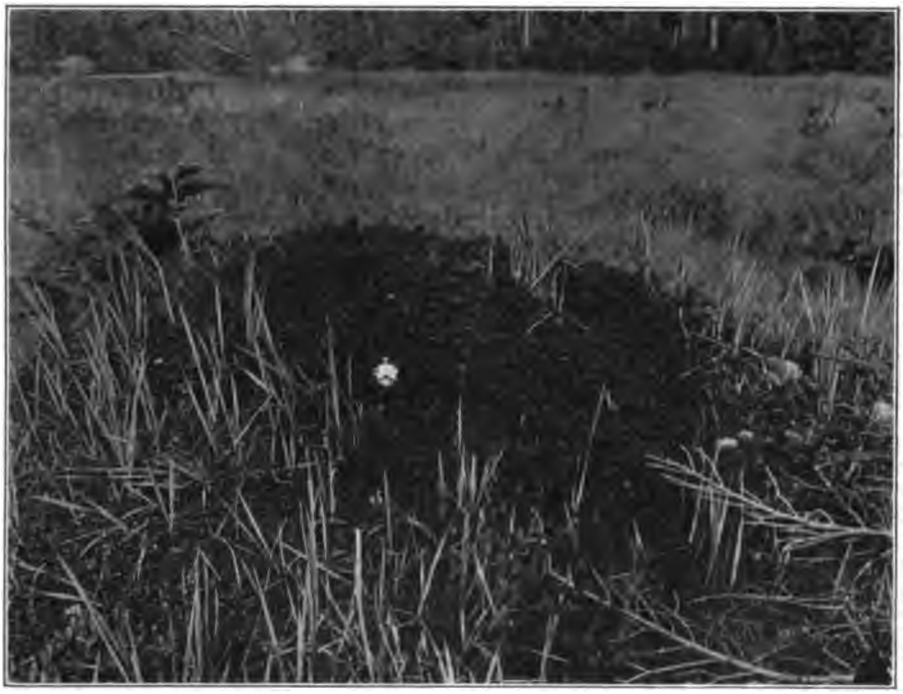

FIG. 15. Crowberry, *Empetrum nigrum,* growing on a boulder in Lake Tear bog; watch as a scale. Note also the young balsam fir.

At the extreme eastern end of the bog is a long tongue of land, slightly higher than the low end towards the lake. This is covered almost exclusively by *Calamagrostis canadensis,* which grows luxuriantly up to 3 feet tall and fruits freely. The bog is peculiar in that no *Juncaceæ* and no *Orchidaceæ* were found in it. They may occur there, but if so they are so infrequent as to make up only a minute fraction of the vegetation. That is true, also, of other plants that are not here recorded from the region.

Collections of invertebrates from the eastern side of the bog, near our thermometers (fig. 5 in Part I) gave the following: spiders, *Pardosa nigripalpis* Em. (*canadensis* Black) and *Epeira trivittata* Em., several grasshoppers, *Melanoplus atlanis* Riley, *Melanoplus femur-rubrum* DeG., *Podisma glacialis glacialis* Scudd. and *Chorthippus curtipennis* Harr., a psyllid, *Psylla strata* Patch (?), a psocid, *Psocus confraternus* Bks., and the bumble bees, *Bombus terricola* Kby. and *Bombus fervidus* Fab. There were numerous young of the grasshopper, *Chorthippus curtipennis* in the low vegetation. It is evident that the spider (*Epeira*) and insects are mainly species which live in the open, rather than in the forest. The presence of *Podisma* here, as well as in the alpine zone, is worthy of special mention on account of its similarity to the case of *Empetrum*. Colvin (loc. cit., p. 130) refers to the small aquatic bivalve molluscs, *Sphærium occidentale* Prine and *Pisidium abditum* Hald., from Lake Tear. Colvin (p. 130) also refers to seeing tadpoles of frogs in this lake.

The artificial opening at our camp, made by the many visitors to the top of Marcy, provided a small open area where a few invertebrates were taken. These were a dragon fly, *Æschna eremita* Scudd., the daddy-long-legs, *Mitopus montanus* Bks., which abounded about our lean-to, and a spider, *Steatoda borealis* Hentz. Along the Marcy trail just above camp a horntail, *Sirex cyaneus* Fab., was taken.

The few openings in the coniferous forest were especially attractive to birds, for they appeared to be more abundant at our camp clearing and at Lake Tear than in the dense forest through which the trails passed. This was very noticeable in case of juncoes and golden-crowned kinglets. Eaton (loc. cit., p. 42) notes a decided preference for slashings, clearing, burnt areas and swamps, on the part of all but fifteen species, which seem to tolerate the thick forest more than others; but even these show some preference for openings. Of these fifteen birds the following occur in the upper part of the balsam covered slopes: Olive-backed thrush, hermit thrush, red-billed nuthatch, brown creeper, *Certhia familiaris americana,* winter wren, myrtle warbler, blue jay and the Canadian ruffed grouse. Colvin (loc. cit., p. 130) mentions a "couple of snipe, which seemed to make their summer home by the shores" of Lake Tear.

DWARF FIR FOREST JUST BELOW TIMBER LINE, 4,890 FEET.—In going up the trail from Lake Tear, or on the other trails up the mountain, the fir forest becomes progressively lower as we approach timber line. The line of demarcation between unbroken forest and alpine vegetation is very sudden as there may be stunted fir trees 7–12 ft. tall at one point, and not 25 feet from them, an unbroken alpine fell-field with only much battered and isolated trees scattered through it, in locally protected places. But as defined elsewhere in this paper, the timber line is the upper limit of continuous forest, and at this point the trees are only 7–12 ft. tall. They are thick, however.

relatively old, and so frequent that off the trail it is difficult to force a passage (figs. 6–7 in Part I). Almost no other tree is found associated with *Abies balsamea,* and only occasionally are there stunted paper birches, *Betula papyrifera.* The latter have all the indications of wind-swept stunting and probably it is mostly to this wind agency that their gnarled appearance is due.

There is no deciduous shrubby undergrowth of any sort in the shade of these sturdy little firs, the forest floor being made up mostly of *Sphagnum acutifolium, Hypnum Schreberi, Dicranum scoparium,* and *Dicranum longifolium,* and perhaps others. In this soft, mossy cushion, like a sponge for holding water, there are a few herbs of which the commonest, the almost exclusive one, is *Oxalis Acetosella.* Next to it in frequency is *Clintonia borealis.* Among these two herbs there are scattered a few others, which in the order of their frequency are:

Solidago macrophylla
Cornus canadensis
Linnæa americana
Chiogenes hispidula
Unifolium canadensis
Ophrys cordata (rare)

No true alpine alpine plants are found here in these shaded nooks which are quite out of the wind, so dense is canopy of the dwarf firs. Yet only a stone's throw above is the open bare summit of Marcy with the Lapland Rhododendron and the other alpine plants growing in the blazing sun, and beaten upon by the full force of the winds.

This fir forest provides shade for a handful of species of herbs from moderate elevations, but not one true alpine plant penetrates down through the barrier of timber line. All the species listed are found much farther down Marcy, most of them quite down to the valley 3,000 feet below. *Oxalis Acetosella* is the dominant one, just as it is in the similar fir forest on the top of Slide Mountain in the Catskills, which has no alpine vegetation.

A comparison with the forest floor herbs found at the lower limits of the pure fir shows that *Cornus canadensis* is there the dominant herb, here replaced by *Oxalis Acetosella. Solidago macrophylla* in both places is common, and *Linnæa* and *Chiogenes* in both places make up a fair proportion of the vegetation. But some other herbs that are in the list on page 206 have not gone up to the edge of the forest, as the wood-sorrel, bunch berry and creeping snow-berry have done. Certain herbs of the fir—and lower down of the spruce—forest, at home in quiet shady places, their roots in a sponge of moss and scarce feeling the terrific winds that blow over the mountain, may as we shall see presently, go out over the bare summit changed in stature, often in color, and in nearly always habit, but still persisting and fruiting. Yet the plants typical of the summit, played upon by all the forces of an apparently uncongenial habitat, do not meet the conditions of the region below timber line well enough to be found there. The single exception is the bog at Lake Tear, already described. To the discussion of the plants of the summit there will be noted the amount and success of this invasion of purely alpine vegetation by these lowland plants. The evidence is all that it is the alpine plants that are isolated and being gradually crowded by these invaders.

The invertebrates of the marginal dwarf forest (fig. 7 in Part I) (Field Station *c*) are represented by a single collection. This included certain insects taken on wing near the tops of the trees, such as black fly, *Simulium hertipes* Fries (?), and two syrphids which were taken hovering among the balsam branches, *Syrphus ribesi* Linn. and *Melanostoma obscurum* Say, and the fly, *Bibio xanthopus* Wied., a characteristic species which hovers in the sun about the margins and over the surface of the dwarf forest. In a warm sunny moment a loud buzzing attracted attention to several horntails, of two species, *Sirex cyaneus* Fab. and *Urocerus albicornis* Fab., which were flying about among the branches, while from the moss and rotten wood of the forest floor was taken an earthworm (*Enchyatrid*), spider, *Tmeticus armatus* Bks., a myriopod, *Conotyla fischeri* Ck., the pupa of a beetle, tipulid larvæ *Tipula,* near *Ignobalis* Low., and small ants, *Leptothorax* (*Mychothorax*) *acervorum* Nyl., subsp. *canadensis* Prov.

Very little is known of the habits and habitats of most of the above listed species. The larva of *Sirex cyaneus* feeds upon the wood of spruce, fir, and hemlock. These are thus distinctly forest species. The larvæ of allied species of *Bibio* live in forest humus. It seems probable on the whole that the collection is distinctly of forest inhabitants.

While it was shown in Part I that timber line is a quite definite thing on the mountain, it was also noted that trees occur in depressions and ravines above it and therefore extend the habitat of forest animals well above 4,900 feet. While these animals live in the dwarf forest, it should not be ignored that they are within easy reach of abundant food, for near them, on the bare summit of Marcy are numerous plants with edible fruits such as blueberry, crowberry, cranberry, etc. Blueberries are eaten by the junco (Judd,[21] p. 81), white-throated sparrow (loc. cit., p. 72) and the Canada grouse (Judd,[22] p. 39). Forbush[23] (p. 10) lists the crowberry, *Empetrum nigrum,* and the bunch berry, *Cornus canadensis,* as plants whose fruits are attractive to birds. The latter plant is found above as well as below timber line. He also notes (loc. cit., p. 15) three species of blueberries, including two species found on Marcy, associated with these low conifers: dwarf blueberry, *Vaccinium cæspitosum* and *Vaccinium canadense.* The dwarf cranberry, *Oxycoccus Oxycoccus*, is listed by Forbush[24] (p. 376) as a plant with fruits edible for birds. McAtee[25] (p. 188) includes the dwarf blueberry in his list of plants useful in attracting birds.

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[21] Judd, S. D., "The Relation of Sparrows to Agriculture," U. S. Biol. Survey Bulletin 15, pp. 1–98, 1901.

[22] Judd, S. D., "The Grouse and Wild Turkeys of the United States and Their Economic Value," U. S. Biol. Survey Bull. No. 24, pp. 1–55, 1905.

[23] Forbush, G. H., "Plants that Attract and Shelter Birds and some that Protect Cultivated Fruit," Mass. State Dept. of Agr. Dept. Circular 13, pp. 4–29, 1919.

Little animal life was noted about these dwarf forests during the few days of observation, but birds and mammals, especially those that conceal themselves on the approach of man, could very easily be overlooked here, and it was almost impossible in walking through the growth to flush or "jump" any animal in it. No vertebrate was found that appeared to prefer the stunted to the taller forests lower down. The species noted were junco, myrtle warbler, chestnut-sided warbler, *Dendroica pennsylvanica,* swamp sparrow, *Melospiza georgiana,* and white-throated sparrow, *Zonotrichia albicollis.* A number of each of the first two were seen, but only one each of the others, except the last which was heard only. Eaton[26] records the following birds from altitudes where this Krumholtz exists: Junco ('14, p. 407); white-throated sparrow ('10, p. 47); pine siskin, *Spinus pinus* ('14, p. 279); myrtle warbler, *Dendroica coronata* ('14, p. 407); black poll warbler, *Dendroica striata,* and Bicknell's thrush ('14, p. 523); and found pine siskins breeding in large numbers near the peaks of Mount Skylight and Mount Marcy. Since the last named species prefers conifers for nesting, it undoubtedly used these stunted trees, the only ones in their breeding area noted by Eaton.[27] Colvin (loc. cit., p. 371) reports footprints of raven, *Corvus corax principalis,* at 5,000 feet and reports (p. 131) shooting a Canada grouse (probably *Canachites canadensis canace*) in the dwarf forest on Mount Skylight. It is probable that there are many of these grouse on Mount Marcy at present; guides testify to this.

About a dozen mouse traps left out for two nights in this low tree growth resulted in getting one red-backed mouse in a dense thicket of conifers near Station *d,* where the trees were about two and a half feet high. Mr. C. F. Batchelder in a letter writes that he found this species in the dwarf forest region on Mount Marcy. It is probable that the animal is permanently established here, at least in the lower part of the area, since the conditions favorable for the little animal are present almost everywhere in the dwarf forest. These conditions are well described by Batchelder[28] (p. 192) as follows: "One may look for it with some confidence in almost any large tract of wet ground that retains its moisture through the summer, but is not subject to serious floods, and which bears a growth of woods sufficiently heavy to afford a dense shade, so that the ground beneath, and the roots of the trees, are covered with a deep carpet of sphagnum. . . . One of the most evident peculiarities of such a spot as this, in Southern New England, is that dense shade and abundant evaporation maintain a temperature during the hottest summer weather that is far below that of the surrounding country." There was food in abundance for red-backed mice in the adjacent alpine growth, consisting of (Merriam,[29] p. 271) berries, roots, and bark. The blueberries that are found abundantly in that region are very probably eaten extensively by the red-backed mouse and other animals of the Krumholtz.

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[24] Forbush, G. H., "Useful Birds and their Protection," Mass. State Board of Agr., p. 1–451, 1913.

[25] McAtee, W. L., "Plants useful to Attract Birds and Protect Fruit," Yearbook Dept. Agr. for 1909, pp. 185–196, 1909.

[26] Eaton, G. H., "Birds of New York," Memoir 12, Part 2, New York State Museum, pp. 1–719, 64 plates, 1914.

[27] Black poll warblers were found breeding near the summit of Mount Marcy and other high mountains nearby (Eaton, loc. cit., p. 418).

[28] Batchelder, C. F., "Some Facts in Regard to the Description of Certain Mammals in New England and Northern New York," Proc. Boston. Soc. Nat. Hist., Vol. 27, pp. 185–193, 1896. See also Batchelder, C. F., "An Undescribed Shrew of the Genus *Sorex,*" Proc. Biol. Soc. Washington, Vol. 10, pp. 133–134, 1896.

No other mammals were found in the region of stunted trees, but at one place a bed or "form" was found, with droppings beside it, indicating the presence of the varying hare, *Lepus americanus virginianus* (Harlan). Guides informed us that hares are common in this region. Colvin (loc. cit., p. 130), however, thinks that the varying hares taken on Mount Marcy are different from those found by him elsewhere in the Adirondacks. He says (p. 370) that the range of the species does not appear to be above 5,000 feet, and he mentions in particular the taking of one on Whiteface Mountain at 4,900 feet. Evidently this region gives a favorable habitat for the species, which prefers (Seton,[30] p. 627) a growth, "so dense that the fox, the lynx, and the wolf have no chance in open chase," and where they have open spaces for sun-baths.

No tracks or other signs of deer were noted in this low conifer growth, but deer are found here at times according to the testimony of guides. Colvin (loc. cit., p. 368) found the fisher, *Martes pennanti pennanti* (Erxleben), in the dwarf forests on Mount Marcy, where, he says, they hunt hares. Batchelder, in a letter, states that the masked shrew occurs here, as elsewhere on the mountain.

ALPINE ZONE 4,920–5,344 FEET.—The summit of Marcy is without forest covering, although there are stunted and gnarled trees scattered all over the mountain-top in protected places. The vegetation, other than trees, is made up of a group of alpine, sub-alpine and other species that are constantly subject to destruction, not only by climate, but by sliding boulders and slabs of rock. The local erosion cuts small gullies (fig. 19) through existing vegetation, and often retards revegetation of older erosion sites. On all the steeper slopes of the mountain above timber line are found large areas where vegetation is putting up a losing fight to cling to the side of the mountain. Some ancient and local group of plants, perhaps surrounding a dwarf tree (16–20 inches high) that may be 65 years old, will, during a spring thaw, be quite suddenly wiped out, leaving the naked site to be subsequently invaded. A host of pioneers then come and make ready the conditions that will support the climax vegetation which stable erosion conditions show to be the final type in the alpine zone (fig. 16).

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[29] Merriam, C. H., "The Mammals of the Adirondack Region," New York, pp. 1–316, 1886.

[30] Seton, E. T., "Life Histories of Northern Animals," New York, Vol. 1 and 2, pp. 1–267, 1909.

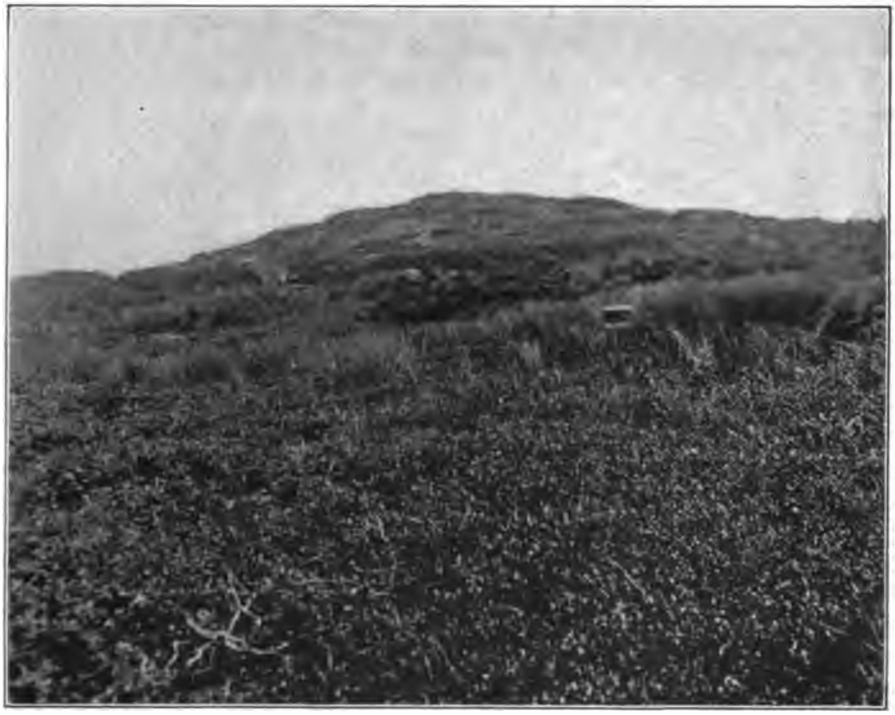

FIG. 16. Climax vegetation in the apine zone.

Upon this conception much of the vegetation of the mountain-top is in a constant state of flux, and it might be difficult or impossible to describe or conjecture what the ultimate type of vegetation would be, nor the steps that lead to that fulfilment. Fortunately there are many less steep places with few chances of destruction overtaking them, and in such is developed to perfection the typical alpine vegetation. But the accomplishment of this state is a tremendously slow and precarious process, and cases of arrested development are only too common. The chances of a rock slide many feet above such a vegetation climax, diverting a rivulet and thus drying up the site, or smothering with sand the edges of it, and all the fortuitous accidents that exposure to terrific winds, snow, and fogs and temperature (June 5, 1919, at the summit the sun temperature out of the wind was 94°; on August 21, at the camp, 4,300 feet, it was 42°), these and other accidents all make the final climax type of vegetation on the mountain top common enough on less steep places, but by no means so common over the whole mountain as it is on Mt. Washington.

The typical vegetation of this region above timber line shows certain well-marked characteristics, has certain kinds of plants always in it, and has quite definite stages in its development. So much of the mountain top is bare rock or loose slabs or boulders, all the soil is from the decomposition of such material, described elsewhere in this paper, that the earliest stages of vegetative covering are necessarily based upon the occurrence of this soil and a suitable water supply. To go one step backward, the organisms that help to break down this rock, and which cover many of them, are the real pioneers in the beginning of the vegetative climax. On many rocks otherwise quite bare, are to be found *Umbilicaria pustulata,* followed often by a tiny accumulation of mineral soil and then the mosses, *Andreæa petrophila* and *Polytrichum strictum.* The two latter often make quite considerable patches along the edges of great, bare boulders, catching small accumulations of soil and adding to such tiny pockets, by their own decay, a nucleus for the establishment of other plants. Where this accumulation of soil goes on long enough to become an inch or two deep and there is available water, we have a largely mineral soil, almost invariably occupied by the deer-hair, *Scirpus cæspitosus* (fig. 17). So common are the conditions that sustain

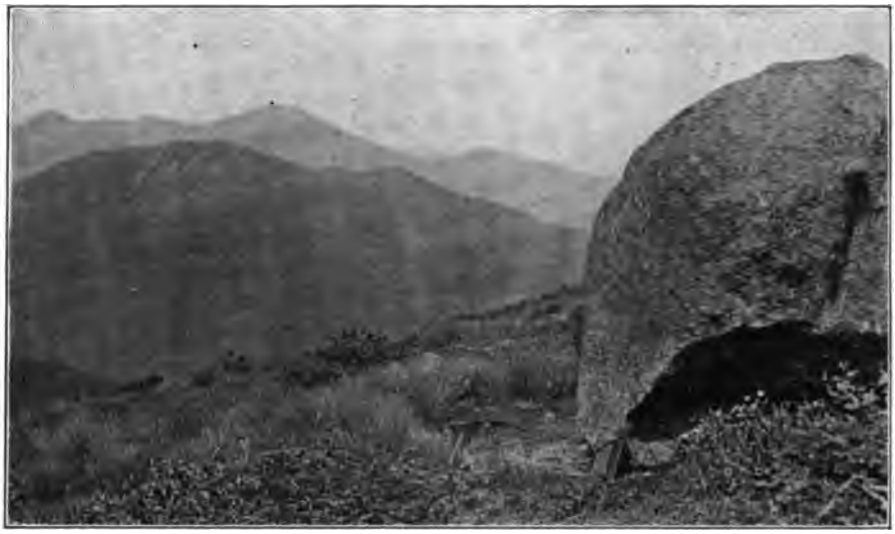

FIG. 17. Early stage in succession in the alpine zone. Deer-hair, *Scirpus cæspitosus,* showing zonation around a seepage spot.

this sedge that it almost appears as if it were the commonest plant of the region, its golden-yellow tips being conspicuous also in many other conditions than this one in which it is apparently the pioneer. Often growing near or on it, and due perhaps to the decomposition of successive generations of it, are found *Cladonia rangiferina* and *Sphagnum acutifolium.* One of the most characteristic features of the mountain-top are the small or large cushions of this moss and lichen fringed by *Scirpus cæspitosus,* and supplying a water soaked environment for the more permanent plants that come after. Sometimes with the *Scirpus cæspitosus,* or alone in similar conditions, *Arenaria grœnlandica* is to be found. Both of them are to be considered pioneers, as the climax type of vegetation hardly ever includes them and grows on an acid substratum which these plants do not need and rarely tolerate.

The stage following the accumulation of the moss-lichen cushion is followed by *Vaccinium uliginosum, Empetrum nigrum* and *Oxycoccus Oxycoccus.* Where the water supply is fairly near and copious, these plants grow luxuriantly and are normally colored, but on drier sites they are reddish or coppery and appear half starved, with poor shriveled fruits. Other plants growing in such places are, in the order of their frequency:

Ledum grœnlandicum
Vaccinium cæspitosum
Agrostis borealis
**Cornus canadensis*
**Trientalis americana*
**Betula papyrifera,* stunted, not over 1 ft. high
Lycopodium Selago
Potentilla tridentata
Chamædaphne calyculata
**Unifolium canadense*
Solidago Cutleri
Vaccinium canadense

This is fairly typical of the region just above the timber line, and in such places, and elsewhere over the mountain-top will be found stunted trees, about 15 inches high of *Picea mariana,* and of the fir, chiefly the latter. These are often half smothered by the dense cushion of sphagnum moss and the plants growing in it, and it is in the "protection" of these trees that most of the plants starred in the list grow. They belong in the forest below timber line and out on the bleak summit they usually, but not always, are found in the protection of these dwarf trees in ravines.

The occurrence of the black spruce here at 4,920 feet elevation, and only above timber line, where it is common quite up to the summit, is peculiar. The same thing occurs on Mt. Skylight, where we collected it only above 4,800 feet, and on Mt. McIntyre, where our records show it as not below 4,700 feet. Diligent search for cones of this spruce on all three mountains was rewarded only on Mt. Skylight, where, at 4,800 feet, a single tree, about 6 feet tall and in a locally protected place, was covered with cones. The black spruce is considered by some botanists merely an ecological variation of red spruce, *Picea rubens,* a stunted form occurring in bogs. In truth the distinction is not sharp and the two trees may readily be confused. But why should black spruce grow in the bogs at lower elevations (it does not grow in the Lake Tear bog at 4,320 feet), and then reappear on the summits above timber line? It is also found, according to Mathews, "Field Book of American Trees and Shrubs" (Putnam, 1915), on Mt. Katahdin, Maine, at 5,215 feet. It seems that this tree must be added to the list of alpine plants which are restricted to the zone above timber line and to certain bogs below it. Such plants here find an environment sufficiently rigorous to keep out most competitors and to delay the migration which has eliminated them from the more favorable places. Unquestionably they are relics of a colder flora following the ice, and, this study indicates, are subject to steady encroachment by the lowland plants to-day.

The rather meagre list of plants characteristic of this alpine zone, that is, just above timber line, could be greatly extended by only a slight rise in elevation. From 4,920 feet up to the summit at 5,344 feet, there are many hundreds of acres, sometimes pure rock slabs nearly bare of vegetation, some few deep ravines with trees in them which reach only to the height that the protecting rock keeps off the winds, some nearly level alpine fell-fields where the flora is more static than elsewhere and alpine species are best developed, and many steep slopes where destruction of local habitats goes on with rapidity and effectiveness. Depending on location and drainage, protection from wind and snow cover, there are acres of this climax type perfectly developed, and many others in the stages of development which have been indicated. At slightly higher elevations (5,050 ft.) and up to the summit, *Diapensia Lapponica* and *Rhododendron Lapponicum* appear in sufficient quantities to be a noticeable percentage of the vegetation.

Two well-marked and rather distinct variations of the typical alpine zone of the mountain demand notice, not alone for their curious assemblage of plants and animals, but because in them species were found not before recorded from above the timber line. These two localities are:

I. Dwarf birch meadow at 5,250 ft.

II. Meadow on S.E. side of mountain at 5,100 ft.

I. *Dwarf Birch Meadow.*—The meadow which we have named for this shrub, and it is the only place on the mountain where the plant was found, is about a quarter of a mile from the summit and on the northeast side of the mountain. It is an incipient glacial cirque, the only cirque on the mountain. On June 5, 1919, a large part of it was covered with snow deep enough and packed enough to walk over, and the margins, for 10–15 feet, fringed with a nearly exclusive growth of dwarf birch, *Betula glandulosa,* then in full flower (figs. 18 and 19).

During our second visit to this meadow in August it was found that the part uncovered by the melting snow consists almost exclusively of *Calamagrostis canadensis,* and not quite so common *Deschampsia flexuosa* and *Carex oligosperma.* This coarse turf, one of the ingredients of which is the same as for the bog at Lake Tear, is dotted with other plants. Many of these are apt to be partly smothered by grass, especially by *Calamagrostis canadensis.* The secondary species in this turf are, in the order of their frequency:

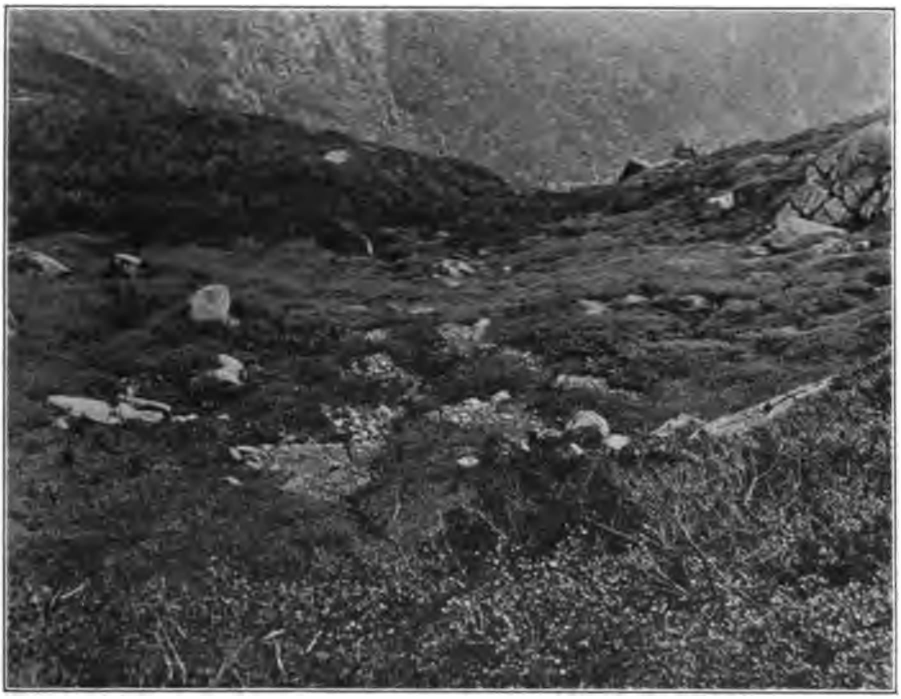

FIG. 18. Dwarf Birch Meadow from above, showing fringe of *Betula glandulosa* in the foregroung. This meadow contains many plants of lower elevations which are invading the alpine zone.

**Gentiana linearis*
Potentilla tridentata
Vaccinium cæspitosum
Vaccinium canadense
**Viola pallens*
**Rubus* (trailing species, no flowers or fruit)
**Spiræa latifolia*
Ledum grœnlandicum
Diapensia Lapponica
Rhododendron Lapponicum
Eriophorum callithrix
Lonicera cœrulea
**Houstonia cœrulea*
Lycopodium Selago

The occurrence of those species starred in the list, together with *Calamagrostis canadensis,* which is a dominant plant in the meadow, is another illustration of the encroachment of plants normally at home at much lower elevations, into the alpine zone. This meadow at 5,250 ft., near the summit of Marcy, and with a northeast exposure which subjects it to the winter winds from that quarter, sustains a fair percentage of plants that might not be expected to survive the rigorous conditions under which typical alpine species grow. *Calamagrostis canadensis* particularly, as the dominant turf grass, very luxuriant and fruiting freely in a short growing season to which its wide distribution at lower elevation would not seem to fit it, is a conspicuous example of what is true of so many other herbs on Mt. Marcy. Of course these comparatively lowland, or at least not alpine plants, are not as yet completely crowding out the true alpines here, except *Calamagrostis canadensis,* but they form a respectable part of the vegetation, and, surrounded by a thicket of *Betula glandulosa,* a true alpine shrub, the inhabitants of this upland meadow form an interesting study. For, isolated in this meadow are enough lowland species, one of them a practically dominant grass, to give a distinctly different aspect to the meadow from that of the

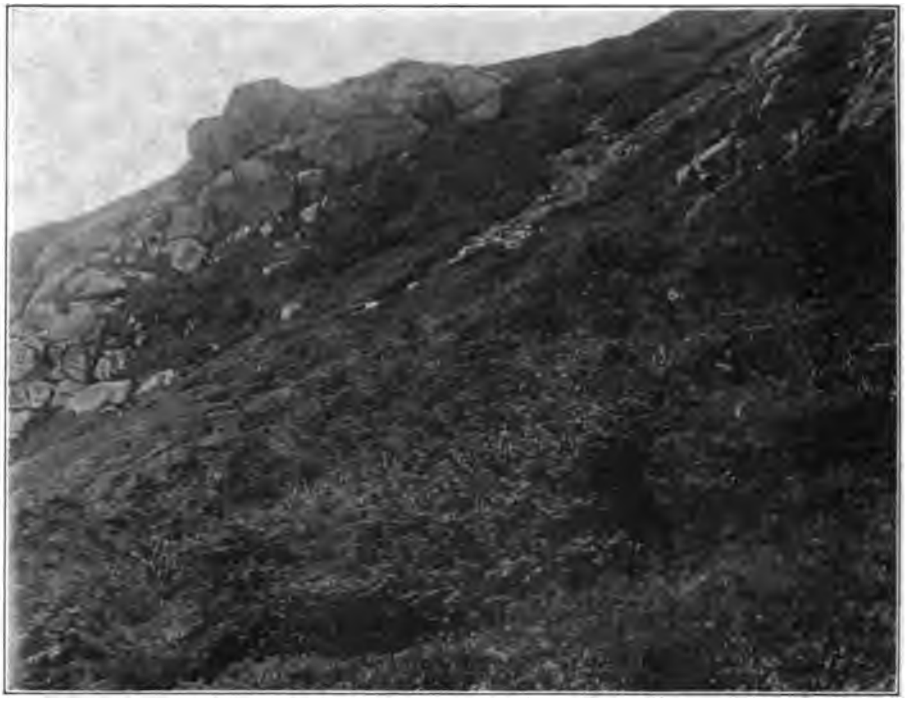

FIG. 19. Looking across Dwarf Birch Meadow, showing incipient cirque character and a gulley. Typical pocket of dwarf fir in a depression in foreground.

surrounding alpine vegetation. The isolation of these lowland species relatively so far above timber line, is matched at only one other place observed by us, on the southeast side of the mountain.

This basin, protected from winds, is particularly favorable for animals from lower altitudes, when once the snow has melted. The collection of invertebrates from this cirque include: the spiders *Clubiona,* and *Pardosa nigripalpus* Em., a staphylinid beetle *Acidota subarinata* Er., a bug *Clastoptera obtusa* (Say), jassids *Philænus spumarius* L., *Deltocephalus sayi* Fh. and *affinis* G. and B., a plant louse, the grasshoppers *Podisma glacialis glacialis* Scudd., *Melanoplus atlanis* Riley and *Cammula pellucida* Scudd., the butterfly *Eurymus pholadice* Godt., and the ants *Formica fusca* L. var. *algida* Wheeler, *Camponatus herculeanus* L. subsp. *ligniperda* Latr. var. *noveboracensis* Fitch. Specimens of *Bombus* were seen which were not taken. Here we see the upward extension of lowland species as in the case of the plants. The jassid *Deltocephalus affinis* is infested with a Dryinid parasite.

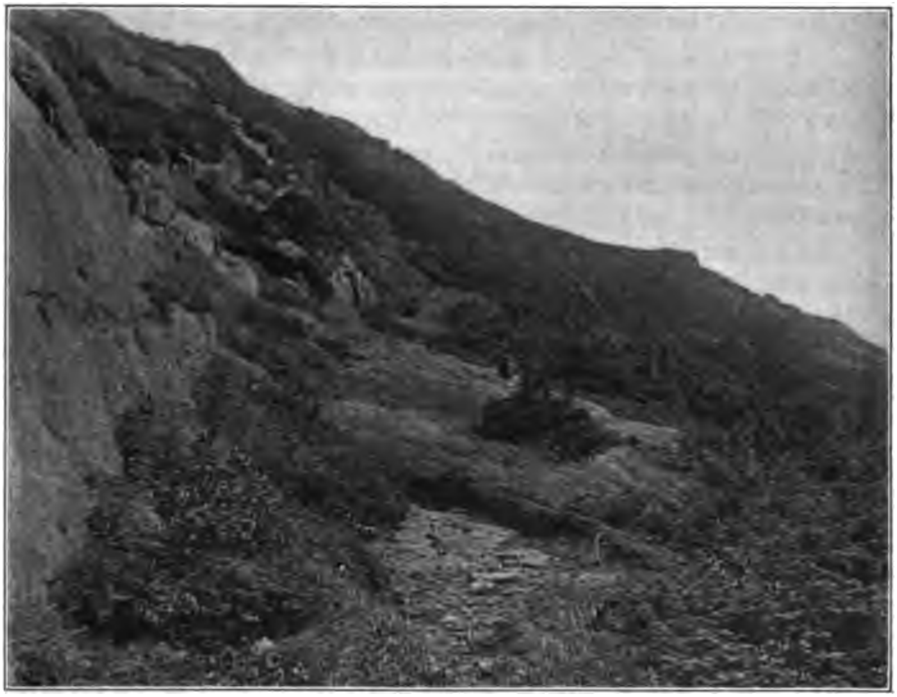

FIG. 20. Meadow on southeast slope at 5,100 feet, containing many lowland plants invading the alpine zone.

II. *Meadow on Southeast Side of the Mountain at 5,100 Feet.*—While the dwarf birch meadow shows some examples of the intrusion of lowland species through the alpine flora, the meadow on the southeast side of the mountain is remarkable for such intrusion. The meadow is about 300 feet long and 20–40 feet wide, rather steep, and faces south. It is northeast of where the trail from Ausable Lakes reaches timber line, and near the base of a large landslip slope that leads directly to the summit. On the west or mountain side the meadow is faced by a steep rock cliff 20–30 feet high, with little or no vegetation on it, except in crevices. On the lower side the meadow is fringed by fir trees, which are themselves bordered, toward the center of the meadow, by alder, *Alnus alnobetula,* a shrub not uncommon elsewhere in the alpine zone. A small rivulet comes out from the cliff about half way up the meadow, and meanders into a small bog-like place scarcely 10 feet square and is then lost by drainage through the loose soil and rock which underlie the region (fig. 20). The topography suggests that the meadow is covered with deep drifting snow in winter.

As in the dwarf birch meadow, the dominant, almost exclusive plant, is *Calamagrostis canadensis* which makes a coarse, dense turf. Near the outer edges of this turf are patches, or sometimes a fringe of *Lonicera cærula, Vaccinium uliginosum* or *Vaccinium cæspitosum, Chamædaphne calyculata, Ledum grœulandicum* and *Spiræa latifolia.* Scattered through the turf are patches of *Deschampsia flexuosa* and along the edges of the cliff and other rocks are fringes of *Carex oligosperma,* which is rather uncommon. The latter sedge was noted in the bog at Lake Tear, but not elsewhere on the mountain. Other plants in this meadow, not arranged in order of frequency of occurrence, but with some notes on them, are as follows:

**Linnæa americana*
Oxycoccus Oxycoccus
**Houstonia cærulea,* also the white flowered form.
**Cornus canadensis,* reddish colored and apparently unhappy.
Solidago Cutleri
**Solidago macrophylla,* common and luxuriant.
Lycopodium Selago
**Clintonia borealis,* not fruiting so freely as below timber line.
**Gentiana linearis,* common
Rubus sp. (the same as in dwarf birch meadow, and without flowers or fruits).
Ribes glandulosum
Potentilla tridentata, perfectly at home along edges of the cliff.
**Veratrum viride,* also scattered all over the summit.
**Doellingeria umbellata,* near the small bog-like center of the meadow.
Nabulus nanus, also scattered all over the summit.
**Blephariglottis dilatata,* this and the next near the bog-like center of the meadow.
Calamagrostis neglecta, also from Lake Tear, rare here.
**Viola labradorica,* rare and only a few seen.
**Carex intumescens,* rare.

There are a few scattered patches of shrubbery in the meadow where individuals are scarcely 2 feet high, and made up of *Amelanchier spicata* and *Viburnum pauciflorum,* the latter not before recorded from Mt. Marcy.

In the list those plants which are starred, as well as *Calamagrostis canadensis, Spiræa latifolia, Deschampsia flexuosa, Amelanchier spicata,* and perhaps *Viburnum pauciflorum,* are all to be considered as intruders from the lowland into a meadow that is well above timber line, and contains a fair percentage of alpine plants. This meadow is the most striking example of what is more or less true of all the summit of Marcy. Nowhere is the elevation great enough nor conditions unfavorable enough so that there is not this encroachment of lowland species up through the timber line and quite over the summit. The small number of true alpine species that are found on the mountain, the great scarcity of some of them, the crowding of the lowland species amongst them—all these make Mt. Marcy a very favorable site to study certain species on the altitudinal edges of their range. With a thousand feet greater elevation, the percentage of true alpines would certainly be much greater, as it is on Mt. Washington, and there would be nothing like the encroachments of lowland species up through the timber line. The summit of Mt. Marcy physiographically, and so far as a well defined timber line is indicative, has unquestioned alpine vegetation upon it. But this is composed of only a relatively small number of alpine plants. When the lowland plants, as in the case of *Viola labradorica, Solidago macrophylla, Clintonia borealis* and many others have a comparatively large exposure of leaf-blade and consequently a somewhat high transpiration rate, it is remarkable that they, as compared to *Ledum* and *Chamædaphne* and *Rhododendron Lapponicum,* and other plants well insured against a too vigorous transpiration rate should have monopolized so much of the summit of Marcy. Bonnier[81] mentions some interesting experiments he has made on the influence of an alpine environment upon plants from the lowland. The external and internal structure as well as the flowers of lowland plants grown at about 8,000 feet elevation became similar to those of alpine plants. He also found that the rate at which oxygen is given off and carbon dioxide taken up is two or three times as much in the higher altitude as in the lowland.

This particular meadow is of chief interest as illustrating, because of locally favorable conditions, such as the protection from the winds afforded by the cliff which borders its western edge, the determined encroachments of the lowland species wherever the opportunity for their survival presents itself. There are hundreds of locally favorable sites for this encroachment on Marcy, such as small ravines, pockets and cracks in the rock, and in nearly every one is to be found these lowland species often associated with a stunted fir or *Picea mariana*. It seems as if the factors that have made the timber line quite definite on the mountain have not created a barrier against the upward extension of those species noted as lowland ones. Except at Lake Tear, already discussed, ***not one case of invasion from above downward*** has been seen by us.

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[81] Bonnier, Gaston, "Le Monde vegetal," Ernest Flammarion, Paris, 1914. (See especially pp. 335–342.)

The collection of animals from this meadow include a daddy-long-legs, *Mitopus montanus* Bks., the spiders, *Lepthyphantes* and *Pardosa luteola* Em., the grasshoppers, *Podisma glacialis glacialis* Scudd., *Melanoplus atlanis* Riley, and *Melanoplus luridus* Dodge (only specimen taken on the mountain), a lygæid bug nymph, the jassid, *Deltocephalus sayi* Fh., the fly, *Bibio xanthopus* Wied., the bumblebee, *Bombus terricola* Kby., and the butterfly, *Argynnis atlantis* Edw. The Bibios were very abundant in the sun, hovering about the margin of the stunted trees and over them. A yellow butterfly, similar to *Eurymus* seen in the dwarf birch meadow, was seen but not captured. Two large brownish butterflies were seen but were not taken. The presence of the subalpine *Mitopus* here is of interest, illustrating the upward extension of a species from lower altitudes as in the case of the leaf hoppers, the butterflies, the bees, and the plants already mentioned.

As a record of what grows on the bare summit of the mountain, the following list of plants is presented. Most of the species in it were noted by Peck in his list in the Adirondack Survey of Colvin, already mentioned, or in his later paper in Bulletin 25 of the New York State Museum, 1898. A few recorded by him were not found, and some recorded by him we are inclined to doubt as inhabitants of the summit at present. A few, in bold-faced type, are here reported for the first time from the region.

FLOWERING PLANTS FROM THE ALPINE ZONE ABOVE TIMBER-LINE ON MT. MARCY[82]

†*Abies balsamea* (a, b, c)
Picea mariana
(*Abies nigra* of Peck's List)
**Juniperus communis*
Cinna latifolia (reported by Peck in 1898)
Cinna abundinacea (reported by Peck in 1898)

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[82] Plants marked * are in Peck's lists but either do not grow there now or were not seen by us.

Plants marked † are obvious encroachments from below timber line. Names in **bold face type** were found by us but not reported by Peck. The letters in brackets, thus (a, b, c) after the names, show in which zones besides the alpine, each species was observed by us: (a)=lower limit of fir forest, 4,250 ft.; (b)=bog at Lake Tear, 4,320 ft.; and (c)=dwarf fir forest just below timber line, at 4,890 ft.

In the account of the vegetation of the summit of Marcy, Peck records that "about forty years ago the little moss plant, *Cassiope hypnoides*, was found by Dr. Parry growing in a sheltered depression on the summit of Mt. Marcy, but it does not

**Stipa canadensis*
(*S. Richardsonii* of Peck's List)
Agrostis borealis
(Probably *A. canina* of Peck's List)
†*Calamagrostis canadensis* (b)
**Calamagrostis Pickeringii*
Calamagrostis Langsdorfii (N. L. Britton, 1892)
Calamagrotis neglecta (b)
Savastana alpina
(*Hierochloe alpina* of Peck's List)
†*Deschampsia flexuosa*
(*Aira flexuosa* of Peck's List)
Poa laxa
**Carex scirpoidea.*
**Carex trisperma* (reported by Peck in 1898)
**Carex canescens* (reported by Peck in 1898)
**Carex brunescens* (reported by Peck in 1898)
**Carex sterilis* (reported by Peck in 1898)
Carex oligosperma (b)
**Carex vitilis* (?)
**Carex concolor*
(*C. rigida Bigelovii* of Peck's List)
†**Carex intumescens** (a)
**Carex paupercula*†
(*c. irrigua* of Peck's List)
Scirpus cæspitosus
Eriophorum callithrix
(*E. vaginatum* of Peck's List)
Juncoides parviflorum
(*Luzula parviflora* of Peck's List)
Juncus trifidus
**Juncus filiformis* (reported by Peck in 1898)
†*Veratrum viride* (b)

appear to have been found there since 1879." Diligent search by us, and by others for several years back for this plant has been unsuccessful. Furthermore none of the larger herbaria of the country has a specimen of Parry's from here. In fact it was on this report that *Cassiope hypnoides* was admitted to the Adirondacks by the manuals. The bulk of the Parry Herbarium is now at Iowa State College and Dr. L. H. Pammel writes that "I do not find that there are any specimens of this species from Mt. Marcy in it." In the herbarium of the Philadelphia Academy of Natural Sciences there is a specimen from "The Adirondack Mts." New York. Coll. J. V. H. MD. Date: July 1879. This specimen is from the herbarium of and appears to be collected by Joseph V. Haberer, a physician of Saquoit, N. Y. Dr. Haberer writes that his specimen of *Cassiope hypnoides* was collected on Panther Mountain and is in the herbarium of Hamilton College.

†*Unifolium canadense* (b)
†*Clintonia borealis* (a, c)
†*Streptopus amplexifolius*
**Streptopus roseus* (reported by Peck in 1898)
†*Blephariglottis dilatata*
(*Habenaria dilatata* of Peck's List)
Salix Uva-Ursi
(*S. Cutleri* of Peck's List)
Betula glandulosa
†*Betula papyrifera* (a, b, c)
Alnus alnobetula
(*A. viridis* of Peck's List)
**Alsine borealis* (reported by Peck in 1898)
Arenaria grœnlandica
Coptis trifolia (a, b)
†**Thalictrum polygamum**
Ribes glandulosum (a)
†*Spriœa latifolia* (b)
(*S. salicifolia* of Peck's List)
†*Rubus strigosus* (a)
**Rubus americanus* (reported by Peck in 1898)
Potentilla tridentata (b)
†*Sorbus scopulina*
(*Pyrus americana* of Peck's List)
†*Amelanchier spicata* (a)
†*Oxalis Acetosella* (a, c)
Empetrum nigrum (b)
†*Viola pallens*
(Probably *V. blanda* of Peck's List)
†**Viola labradorica**
**Epilobium angustifolium*
†*Cornus canadensis* (a, c)
Rhododendron Lapponicum
**Kalmia glauca*
Ledum grœnlandicum (b)
(*L. latifolium* of Peck's List)
Chamœdaphne calyculata
(*Cassandra Calyculata* of Peck's List)
†*Chiogenes hispidula* (a, b, c)
Vaccinium canadense
(*V. pennsylvanicum* of Peck's List)
Vaccinium cœspitosum (b)
Vaccinium uliginosum (b)

Oxycoccus Oxycoccus (b)
†*Gentiana linearis* (b)
Diapensia Lapponica
**Melampyrum latifolium*
(*M. americanus* of Peck's List)
**Chelone glabra* (reported by Peck in 1898)
**Rhinanthus Crista-galli*
†*Houstonia cœrulea* (b)
†*Linnæa americana* (a, b, c)
(*L. borealis* of Peck's List)
Lonicera cœrulea (b)
†**Viburnum pauciflorum**
†*Trientalis americana* (b)
†**Doellingeria umbellata**
Solidago Cutleri
(*S. virgaurea alpina* of Peck's List)
†*Solidago macrophylla* (a, c)
(*S. thyrsoidea* of Peck's List)
Nabulus nanus
**Nabulus Bootii* (reported by Peck in 1898)

Of the 80 species in this list, 21 reported by Peck may have disappeared or at least were not seen by us, and 7 rather conspicuous plants, which such a careful botanist could scarcely have missed, have apparently come into the flora. Of these 7 it is significant that 4 are certainly encroachments from lower down the mountain, and that the others are not true alpine plants, although of northern affinity.

Taking the mountain top above timber line as a whole, we find that the species of lowland affinities that have come up through the upper limit of the forest number at least 30, that the true alpines are probably 23 species, which leaves about 23 which it is scarcely safe to assign to either group. So far as Marcy is concerned, the latter do not occur anywhere else except above the timber line, and a few at Lake Tear bog, but in other regions they are more generally distributed. Peck reported not more than 16 true alpine or subalpine species in 1879 and our studies indicate only a somewhat greater number. This mountain-top, with an alpine aspect, is so then, not wholly by virtue of the alpines on it, but by the encroachment of plants from the lowland, which in the conditions above timber line, assume quite different characters from their usual lowland ones; on the other hand the alpines have not been found invading the lower elevations. The mixture of these two elements and a third make up the flora of the summit.

The third element is one apparently neither alpine or lowland. So far as Marcy is concerned, the plants comprising it occur almost exclusively above timber line, and some in the bog at Lake Tear, but in other parts of the northeastern states they are bog plants or those of open, rocky places, but not necessarily inhabitants of regions above timber line. Among these are *Calamagrostis neglecta, Carex oligosperma, Coptis trifolia, Ribes glandulosum, Ledum grœnlandicum, Chamædaphne calyculata, Vaccinium canadense, Oxycoccus Oxycoccus,* and *Lonicera cœrulea.* These and perhaps a few others, while they are common plants on the summit, do not appear to have the significance ecologically that the contrasting alpine and lowland elements certainly have in the vegetative covering of the summit of Mt. Marcy. As to the factors that control the disappearance of well-known plants from the summit such as *Cassiope* and *Phleum pratense* not much is known. The latter was found by Peck but not seen again, and he reported that the orchid *Blephariglottis dilatata,* originally found there by him in 1879, had disappeared. We found it there in fair quantity in at least one locality above the timber line but failed to see *Phleum pratense.* There seem to be, in other words, many plants from the lowlands that come out over the summit of Marcy, survive a few seasons and then pass away.

The summit, so far as animals are concerned, may be considered as an elevated island of open in a sea of balsam forest. Viewed *from above* both of these openings in the forest, Lake Tear and Marcy, show clearly defined concentric zonation; about the lake this is nearly on the same plane, but on the mountain it is on successive elevations. The main animal habitats range from the extensive area of stable solid rock, supplemented by a large area of unstable loose rock in the avalanche region on the southeastern slope, onward through a meadow stage (fig. 16) to the heath or blueberry shrub stage, which may be considered the climax of the alpine area. The animals which live among the stunted balsam firs of the ravines and protected places have already been considered in the section on the dwarf fir forest. The three strictly alpine habitats are thus bare rock, meadow and the heath. The heath is apparently the main habitat of the invertebrates; the vertebrates apparently pay little attention to these minor differences. Local conditions have differentiated somewhat the meadow habitat, especially at two localities. One is in the cirque on the northeastern slope at about 5,200 ft., and called the dwarf birch meadow and the other is the grass meadow on the southeastern slope at about 5,100 feet, not far from the base of the extensive avalanche slope (fig. 19 and fig. 2 in Part I), both of which have been described above under separate headings. The dwarf fir trees and occasional prostrate black spruce have no doubt characteristic animals associated with them, but this problem was not given special attention.

Scudder[33] observes that in the White Mountains of New Hampshire the three zones, forest, krumholtz and alpine "correspond, in the characteristics of their inhabitants, to the Canadian, the Hudsonian, and the sub-arctic or Labradorian faunas."

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[33] Scudder, S. H., "The Distribution of Insects in New Hampshire," Final Rep. Geol. N. Hamp., pp. 331–380, 1874.

The miscellaneous collections of invertebrates which were taken above timber line will be listed first, and later those of special localities or habitats. At about 5,100 feet above timber line were taken two spiders, *Pardosa musicola* Em., and *Pardosa luteola* Em., and the carabid beetle, *Platynus supripennis* Say. These spiders are species of which Emerton[84] (p. 144) states, "Live on mountain tops down to and below the trees, in bogs in Maine, in New Foundland and Labrador." Other collections from above timber line included an ichneumon, *Lissonota punctulata* (Cress), the grasshopper, *Melanoplus atlanis* Riley, and the fly, *Bibio xanthopus* Wied., and a spider with an egg mass, *Pardosa musicola.* In a grassy area near the top of the mountain two specimens of the grasshopper, *Camnula pellucida* Scudd. were taken. At about 5,280 feet was secured a pair of copulating wingless greenish alpine grasshoppers, *Podisma glacialis glacialis* Scudd., the characteristic alpine grasshopper of the mountain. This is one of the few invertebrates previously recorded from the alpine area. Scudder[85] ('97, p. 100) records it from Marcy at 5,400 feet, an elevation greater than that of the mountain! In the White Mountains he records it frequenting the "close branches of the dwarf birch, *Betula nana* [*B. glandulosa*], and is rarely or never seen on the ground." He also records it from Chateaugay Lake, in the Adirondacks at 2,000 feet. A bumble bee, *Bombus terracola* Kby., was taken at about 5,000 feet. A specimen of the horntail, *Urocerus albicornis* Fab., was taken near the top of the mountain in a grassy area, where it had probably flown from some patch of dwarf forest.

Two series of collections from among the heath plants are worthy of special mention. At about 4,900 feet among the heath plants, *Vaccinium, Ledum,* and others, in the vicinity and above Field Station *d,* the following were collected: the spiders, *Pardosa luteola* Em. and *Pardosa diffusa* Em., *Pardosa uncata* Thor., the grasshoppers, *Chorthippus curtipennis* Harr., *Camnula pellucia* Scudd., *Podisma glacialis glacialis* Scudd., *Melanoplus atlanis* Riley, a tachinid fly, *Peleteria prompta* Meig., a syrphid fly, *Syrphus torvus* O. S. and two ichneumons, *Amblyteles funestus* (Crees) and *A. pectifrons* Cress, and the butterfly, *Polygonia faunus* Edw. At about 5,300 feet among blueberries and *Cladonia* the spiders, *Pardosa ulteola* Em. and *Pardosa musicola* Em., a daddy-long-legs, *Mitopus montanus* Bks., the greenish wingless grasshopper, *Podisma glacialis glacialis* Scudd., the grasshoppers, *Melanoplus atlanis* Riley and *Camnula pellucida* Scudd., the bug, *Mabis ferus* Linn., two jassids, *Deltocephalus sayi* Fh. and *affinis* G. and B., a beetle, *Lebia ornata* Say (var.), the cerambycid beetle, *Leptura canadensis*

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[84] Emerton, J. H., "Geographical Distribution of Spiders in New England," Appalachia, Vol. 13, pp. 143–159, 1914.

[85] Scudder, S. H., "Revision of the Orthopteran Group Melanopli (Acridiidæ) With Special Reference to North American Forms," Proc. U. S. Nat. Mus., Vol. 20, pp. 1–421, 1897; "The Alpine Orthoptera of North America," Appalachia, Vol. 8, pp. 1–21, 1898.

Fab. (the larva feeds on spruce), *Coccinella transversoguttata* Fab., a fly, *Bibio xanthopus* Wied., an ichneumon, *Pezomachus,* and an ant, *Formica sanguinea* Lats., *aserva* Forel. The presence of *Mitopus* above timber line, and also at our camp in the forest is worthy of mention. This phalangid was first recorded from the White Mountains. Mr. Nathan Banks, the author of the species, writes in a letter, "I have since seen it from Maine, several from Province of Quebec (about central part), and Nova Scotia, now yours from Mt. Marcy. Nothing is known of its habits, except that it is sub-alpine." And we may now also add alpine. It was also taken in the grassy meadow on the southeastern slope. It is probably, in the alpine area, mainly an inhabitant of the stunted balsam. The specimen of *Deltocephalus affinis* is parasitized by a Dryinid.

In summarizing the alpine invertebrates we observe that very little is known about certain species, so that no generalization can be based upon them. Others are well-known species of extensive geographic range and in no way peculiar or restricted to these mountain conditions. A few species are in this region mainly restricted to these alpine or bog openings. Faunistically these are the following: spiders, *Pardosa musicola* Em., *Pardosa luteola* Em., *Pardosa uncata* Thor., *Lycosa albohastata* Em., and the alpine grasshopper, *Podisma glacialis glacialis* Scudd.

If, however, we group these alpine species ecologically, as an alpine association, we may include not only the preceding species but also the following: *Melanophus atlanis* Riley, *Melanophus Femur-rubrum* DeG., *Camnula pellucida* Scudd., *Bombus terricola* Kby., *Bombus fervidus* Fab. As a marginal form, between the forest and the alpine open, is the fly, *Bibio xanthopus* Wied. Further studies should increase the number of species as well as a knowledge of their status in such conditions.

Special attention is called to the fact that the greatest lack in our knowledge of these alpine animals is of their life histories, the detailed relations to their environment, and the relation of these animals to one another—their community relations.

No evidence of permanent residents among vertebrate life were found by us in the alpine area, but some birds visit the region. A junco was seen near the summit, and Eaton ('10, p. 47) says that juncoes visit the top to feed on lunches left by tourists. At one time several barn swallows (*Hirundo erythrogastra*) flew over, showing no tendency to linger, and their presence was probably not due to any conditions at the mountain top. Colvin (loc. cit., p. 95) reports seeing hundreds of snow buntings, *Plectrophenax nivalis nivalis,* near the top in winter, and saw two eagles, very probably bald eagles, *Haliæetus leucocephalus leucocephalus,* fly up from near the mountain top. Eaton (loc. cit., p. 44) notes one flying over Haystack Mountain.

Mr. C. F. Batchelder in a letter states that he found four species of mammals on this barren peak region. These were: Red-backed mouse, *Evotomys gapperi gapperi* (Vigors), white-footed mouse, *Peromyscus maniculatus gracilis* Le Conte, masked shrew, *Sorex personatus personatus* Geoffrey, and the big-tailed shrew, *Sorex dispar* Batchelder (Batchelder, '96, p. 133 and '11). The latter was taken here in a rock crevice at an altitude of 5,300 feet.

Colvin (loc. cit., p. 368) observed a fisher, *Martes pennanti pennanti* Erxleben, on Mount Marcy in the winter and shows how this animal might frequent this region even in winter when he tells of their speeding out on icy rocks, and passing safely across glary surfaces of avalanche-swept mountain sides, when pursued by dogs.

(*To be concluded*)

Part III will contain the remainder of the paper, including a map and discussion of tree distribution in relation to exposure, data on the rate of tree growth above and below timber line, an analysis of the vegetation in accordance with Raunkiaer's growth forms, and a summary.

REVIEWS

The Relative Length of Day and Night

Garner and Allard's discovery of the influence of the relative length of day and night on the growth and reproduction of plants[1] adds a hitherto unrecognized factor to the environmental complex. The possibilities which this factor offers for ecological research appear more promising than almost any since Briggs and Shantz found the wilting coefficient of soils.[2]

The importance of light has of course long been recognized, and a few years ago Briggs and Shantz found in studying transpiration that solar "radiation may then be looked upon as the primary causative factor in cyclic changes."[3] Klebs, while working on the problem of rhythm, succeeded in making beech grow continuously in artificial light.[4] Bonnier[5] found that continuous illumination (artificial), as compared with alternate light and darkness, produced marked changes in the form and structure of the plant. The green color was made much more intense, extending to the stems, and the flowers were more highly colored. The surprising part of Garner and Allard's discovery is therefore not that light plays such an important part, but that the relative length of day and night should exercise such an influence on growth and reproduction.

Garner and Allard do not attempt to explain the physiological causes of what they found. It would be interesting to know just what influence the length of daylight has upon the metabolism of the plant to cause such profound changes in vegetative growth and flowering. The effect appears to be the same as variations in the nitrogen and carbohydrate supply. We know that a large supply of nitrogen induces vegetative growth at the expense of flowering, and that a low nitrogen and high carbohydrate supply reduces growth in size and stimulates flowering.[6] Is it possible that the daylight causes an increased absorption of nitrogen? The similarity of the two effects opens up a most promising field of study.

---

[1] Garner, W. W., and Allard, H. A., "Effect of Relative Length of Day and Night and other Factors of the Environment on Growth and Reproduction in Plants," Jour. Agr. Res., 18: 553–606, March, 1920.

[2] Briggs, L. J., and Shantz, H. L., "The Wilting Coefficient for Different Plants and its Indirect Determination," U. S. Dept. Agr. Bur. of Plant Industry, Bul. 230, 1912.

[3] Briggs, L. J., and Shantz, H. L., "Hourly Transpiration Rate on Clear Days as Determined by Cyclic Environmental Factors," Jour. Agr. Res., 5: 583–649, Jan., 1916.

[4] Klebs, G., "Ueber der Rhythmik in der Entwicklung der Pflanzen," Sitzungsberichte der Heidelberge Akademie der Wissenschaft, 23 Abhandlung, 1911; "Ueber das Treiben der einheimischen Baume, speziell der Buche," Abh. d. Heidelb. Akad. d. Wiss. Math.-Naturw. Kl., 3 Abhandl., 1914, Rev. Plant World, Vol. 18, No. 1, p. 19, 1915, Forestry Quarterly, Vol. 13, No. 3, p. 382, 1915, and Vol. 14, No. 1, pp. 83–85, 1916.

[5] Bonnier, Gaston, "Le Monde végétal," E. Flammarion, Paris, 1914 (see pp. 318–320).

The major part of the experiments described consisted of artificially reducing the length of the day by placing the tested plants in specially constructed darkened houses for a certain part of the early morning and late afternoon, while control plants were left out of doors continuously. The plants tested were several varieties of soy bean and of tobacco, aster (*A. linariifolius* L.), climbing hempweed (*Mikania scandens* L.), beans, ragweed (*Ambrosia artemisiifolia* L.), radish, carrot, lettuce, *Hibiscus moscheuotos* L., cabbage, violets (*Viola fimbriatula* Sm.), and early goldenrod (*Solidago juncea* Ait.). The length of day given the test plants was generally from 9 A.M. to 4 P.M., though some had as long an exposure as from 6 A.M. to 6 P.M., and others as short as from 10 A.M. to 3 P.M. With the plants which bloom in the shorter days of late summer the artificially shortened days produced blooming in the early summer. This was particularly true of the soy beans and Maryland Mammoth tobacco. Connecticut broadleaf tobacco on the other hand blossomed at nearly the same time in the test plants and controls. With the climbing hempweed, which normally blossoms from July to September, the test plants, exposed from 9 A.M. to 4 P.M., failed to blossom at all, while the controls behaved normally. With the radish, the test plants developed slowly and finally died; the same occurred with lettuce. In *Hisbiscus moscheuotos* and cabbage the test plants did not blossom, while the controls did. The test plants of violets produced both purple petaliferous and cleistogamous flowers, the controls only the latter kind. With early goldenrod both test plants and controls blossomed at the same time. In general the vegetative growth of all plants was proportional to the length of exposure to light.

The experiments show that for the species studied, flowering and fruiting can be attained only when the length of day falls within certain limits. Some species and varieties respond to short days, and still others respond to all lengths of the day prevailing in the latitude of Washington.

Confirmation of the outdoor experiments was secured in winter by using electric light of comparatively low intensity in a greenhouse to prolong the day. In spite of low intensity of the light—bulbs of 32 candle power were used—a number of plants which did not blossom in the control house were made to flower. Among these were *Iris florentine*, spinach, cosmos, radish, and violets. Plants requiring short days for flowering, such as Maryland

---

[6] Kraus, E. J., ad Kraybill, H. R., "Vegetation and Reproduction with Special Reference to the Tomato," Oregon Exp. Sta. Bull. 149, 1918. Bot. Abs., Vol. 1, entry 1402, Jan., 1919.

Mammoth tobacco, *Freesia refracta,* lima beans, and beggar-ticks (*Bidens frondosa* L.), blossomed in the control house but not in the one which was illuminated. Strangely enough the cosmos in the lighted house averaged 60 inches in height as against only 30 inches in the control house—a remarkable stimulus for light of low intensity!

Extreme variations in soil moisture were found to have no effect on the time of flowering. Reducing the intensity of the light by artificial shading was also ineffective. It was also found, curiously enough, that exposing plants to two periods of illumination daily was vastly less effective in inducing blossoming than a single exposure.

The authors, on page 603, tentatively formulate the following principle: "Sexual reproduction can be attained by the plant only when it is exposed to a specifically favorable length of day (the requirements in this particular varying widely with the species and variety), and exposure to a length of day unfavorable to reproduction but favorable to growth tends to produce gigantism or indefinite continuation of vegetative development, while exposure to a length of day favorable alike to sexual reproduction and to vegetative development extends the period of sexual reproduction and tends to induce the 'ever-bearing' type of fruiting."

The bearing of the experiments on plant distribution is evident. Plants requiring the short days of late summer for flowering and fruiting are unable to establish themselves in northern latitudes because of the low temperature accompanying the favorable length of day. Similarly, plants requiring long days cannot flower in the tropics. This information will unquestionably be of great practical value in agriculture, enabling the better selection of plants capable of producing the maximum amount of vegetable matter or of seed.

The work of Garner and Allard tends to explain many phenomena which were difficult to understand without presupposing an inherent rhythm in plants. For example, the autumn of 1914 in northern Maine was particularly warm, without night frosts; and yet the leaves took on their autumn coloring and fell from the trees, probably on account of the short days. On the other hand there are contradictory phenomena which are probably explainable on the grounds of the wide range of daylight required by certain species and the influence of temperature within this range. For example, living plants of Lapland rhodendron (*Rhododendron lapponicum*) and *Diapensia lapponica* which were found on Mt. Marcy in full flower on June 5, 1919, were collected and brought to the Brooklyn Botanic Garden. These same plants flowered again on April 20, 1920, at a considerably shorter length of day than in their native surroundings.

The results of the experiments above reviewed can readily be supplemented by data on the time of flowering of different plants in different latitudes. The length of day is already known, and can be found in the

"Smithsonian Contributions to Knowledge," V. 21, pp. 114–119, 1876, which gives tables showing the time of sunrise and sunset at ten day intervals through the year for various latitudes in North America. There is rather scanty data on the exact dates of blooming, particularly for spring plants which under favorable conditions bloom again in the fall.

Dr. C. V. Piper, in charge of Forage Crop Investigations in the Bureau of Plant Industry, is much interested in Garner and Allard's discovery, and has written to the reviewer that this "opens a very fascinating new field for ecological work and one in which it seems to me your society (the Ecological Society) might well undertake the systematic collection of data." He suggests for each species of plant the following list of observations:

Location
Altitude, if considerable
Date of first blossom
Date of full bloom
Date of last blossom
Percentage of fruit to blossom—small—medium—large
Date of second flowering in fall, if it occurs.

Since such data will be of unquestionable value in determining the influence of the relative length of day and night on the reproduction of plants, it is hoped that as much as possible will be collected and sent to the authors of the above paper.

Is it not more than probable that the relative length of day and night influences animals as well as plants, and has a direct bearing on such phenomena as periodic hibernation and migration. Garner and Allard's work therefore opens a fascinating field not only for the botanist, but for the zoologist.

BARRINGTON MOORE

PROCEEDINGS

PACIFIC MEETING OF THE ECOLOGICAL SOCIETY OF AMERICA

at Seattle, June 18, 1920.

The Ecological Society met in joint session with the Western Society of Naturalists at 9 A. M. on Friday June 18. The program was as follows:

Weed Invasion of Original Bunch Grass Areas. F. L. PICKETT, Department of Botany, Washington State College, Pullman, Washington. (Read by Title) E. S. A.

Stagnation in Douglas Fir. J. V. HOFMANN, U. S. Forest Service. E. S. A.

The Preservation of Natural Conditions for Ecological Study. VICTOR E. SHELFORD, University of Illinois, Urbana, Ill. E. S. A.

Biological and Physical Agencies affecting Distribution, and the Survival of Plants in New Habitats. D. T. MACDOUGALL, Desert Laboratory, Carnegie Institution, Tucson, Ariz. (To be published in ECOLOGY.) E. S. A.

Some Factors in Evergreenness in the Puget Sound Region. GEORGE B. RIGG, Department of Botany, University of Washington, Seattle. (To be published in ECOLOGY.) E. S. A.

The Habits of Asellus tomalensis; An Ecological Study. P. KONTTAS, Department of Biology, Reed College, Portland, Oregon. Introduced by H. B. Torrey. (Read by title.) W. S. N.

Problems in Floral Dominance in the Open Sea. W. E. ALLEN, Scripps Institution for Biological Research, La Jolla, California. (To be published in ECOLOGY.) E. S. A.

The Seasonal Distribution of Appendicularia. CHRISTINE E. ESSENBERG, Scripps Institution for Biological Research, La Jolla, California. (Read by Dr. Wm. E. Ritter.) W. S. N.

Remarks on Echinoderm Hybridology. H. H. NEWMAN, University of Chicago, Chicago, Illinois. (Read by Title.) W. S. N.

Case Building and Habit Formation in Caddis Fly Larvae. J. H. MALARKEY, Department of Biology, Reed College, Portland, Oregon. Introduced by H. B. Torrey. (Read by Title.) W. S. N.

The Cross Fertilization of Orthocarpus pusillus by Ants. TREVOR KINCAID, Department of Zoology, University of Washington, Seattle, Washington. E. S. A.

The Life History of Aplodontia. C. A. HUBBARD, University of Washington, Seattle, Washington. E. S. A.

At a Symposium on "*The Animal and Plant Resources of the North Pacific Ocean*" held Thursday, June 17, at 2 P. M., the following paper was contributed by the Ecological Society:

Ocean Pasturage and Ocean Fisheries. W. E. Allen, Scripps Institution for Biological Research, La Jolla, California. (To appear in Ecology.)

There was no business meeting of the Society.

A. O. Weese, *Secretary.*

Tentative Program of 1920 Meeting

University of Chicago, Dec. 28–31, 1920.

Tuesday, Dec. 28.
10 A. M. Session for Papers of General Ecological Interest.
2 P. M. Presidential Address.
6 P. M. Dinner for all Ecologists.
Wednesday, Dec. 29.
10 A. M. Session for papers of General Ecological Interest.
2 P. M. Joint Session with the American Society of Zoologists.
Thursday, Dec. 30.
10 A. M. Joint Session with the Botanical Society of America.
2 P. M. Session for papers of General Ecological Interest.
3 P. M. Reports of Committees. Business Session.
Friday, Dec. 31.
10 A. M. Joint Session with the Association of American Geographers; invitation program of four papers.

All members desiring to present papers should, as soon as possible, send to the Secretary the following data: Title, short abstract, time required for presentation, facilities required for presentation, session preferred.

ANNOUNCEMENT

The arrangement by which The Plant World is continued under the name *Ecology*, as the official publication of the Ecological Society of America, will not affect the previously existing arrangements for supplying back numbers and sets of the former journal, and the separates and other publications which have recently been offered. It is not possible to supply the first seven volumes. Volumes 10 and 11 can be supplied only in incomplete condition. All other volumes are $2.50 each. Single numbers are 30 cents each. All separates and publications can be supplied at previously advertised prices. A price-list of publications will be sent on application. All paper should be made payable to The Plant World and all orders should be addressed to

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THE ECOLOGICAL SOCIETY OF AMERICA was founded in 1915 for the purpose of giving unity to the study of organisms in relation to environment, as a means of furthering intercourse between persons who are approaching widely different groups of organisms from closely related points of view, for the stimulation of ecological research, and to assist the development of the utilities which may be served by ecological principles.

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ECOLOGY

Vol. I OCTOBER, 1920 No. 4

LIFE HISTORY AND ECOLOGY OF THE PIGMY SUNFISH, ELASSOMA ZONATUM

R. L. Barney
Director, U. S. Fisheries Biological Station, Beaufort, N. C.
and
B. J. Anson
Assistant, U. S. Bureau of Fisheries

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In the prosecution of studies of the relation of fish to mosquito control in the delta region of the Mississippi, observations were made on the pigmy sunfish, *Elassoma zonatum,* which serve to extend our knowledge of this smallest representative of the spiny-rayed fishes.

The writers were engaged as representatives of the United States Bureau of Fisheries which had entered into cooperation with the United States Bureau of Entomology, and the observations were made at the field laboratory of the latter Bureau, at Mound, Louisiana.[1]

Literature

The literature on the *Elassoma* genus, aside from publications on the distribution and taxonomy of its species, is very limited. *E. zonatum* was

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[1] We are indebted to Dr. W. V. King and Mr. Haw Kirkpatrick of the U. S. Bureau of Entomology, respectively, for the photo-micrographs used in this study and the pictures that appear herewith.

[**Ecology,** Vol. I, No. 1 (pp. 1–70), was issued July 7, 1920; Vol. I, No. 2 (pp. 71–138), August 16, 1920; Vol. I, No. 3 (pp. 241–311), October 22, 1920.]

originally described by Jordan[2] in 1877 from a specimen taken in the Little Red River, Arkansas, in a collection of Professor Henry S. Reynolds.

In 1884, the same author[3] gave a brief systematic description of *Elassoma zonatum* in the publication of a list of fishes collected near New Orleans by Dr. R. W. Shufeldt. In a list of fishes taken in Lake Jessup and Indian River, Florida, by R. E. Earll, Jordan[4] (1884) gives the original description of *E. evergladei*

A. J. Woolman[5] (1890) in a report on the indigenous fishes of central Florida mentions *E. evergladei* and gives a description of the species. Jordan and Evermann[6] (1896) give a systematic description of the two species of *Elassoma evergladei* and *zonatum,* and note their general distribution as follows:

E. evergladei.	"Georgia and Florida."
E. zonatum.	"So. Ill. to Texas; La. and Ala. Not very common and only in still waters of small extent, variable."

Dr. Einar Lönnberg[7] has published descriptive notes on an *Elassoma* found at Orlando, Florida, and named provisionally by him *E. orlandicum.* With the systematic description of the particular fish he found he gave some cursory observations on its breeding season and eggs.

Dr. H. M. Smith[8] (1907) gives a key for the determination of the species of *Elassoma* and also discusses the distribution of *E. zonatum* in North Carolina. He notes that this species is found co-habitant with *Umbra* and various cyprinodonts (*Gambusia, Heterandria,* etc.).

Forbes and Richardson[9] (1908) published a systematic description of *E. zonatum* with a note on its occurrence in Illinois.

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[2] Jordan, David S.: "Contributions to North American Ichthyology Based Primarily on the Collections of the U. S. National Museum," p. 50. Washington, 1877.

[3] Jordan, David S.: "List of Fishes Collected in the Vicinity of New Orleans by Dr. R. W. Shufeldt, U. S. A." Proceedings, U. S. National Museum, Vol. VII: pp. 318–322, Washington, 1884 (1885).

[4] Jordan, David S.: "List of Fishes Collected in Lake Jessup and Indian River, Florida, by R. E. Earll, with Descriptions of Two New Species." Proceedings, U. S. National Museum, Vol. VII: pp. 322–324. Washington, 1884 (1885).

[5] Woolman, Albert J.: "A Report on the Rivers of Central Florida Tributary to the Gulf of Mexico, with List of Fishes Inhabiting Them." Bulletin, U. S. Fish Commission, Vol. X: pp. 293–302, 1890 (1892).

[6] Jordan, David Starr, and Evermann, Barton Warren: "The Fishes of North and Middle America." Bulletin 47, U. S. National Museum, Vol. 1: p. 982. Washington, 1896 (1898).

[7] Lönnberg, Einar: "List of Fishes Observed and Collected in South-Florida." Öfversigt af Köngl. Vetenskap-Akademiens Förhandlingar, No. 3, pp. 109–131. Stockholm, 1894.

[8] Smith, Hugh M.: "The Fishes of North Carolina." North Carolina Geological and Economic Survey, Vol. II: p. 228. Raleigh, 1907.

[9] Forbes, Stephen Alfred, and Richardson, Robert Earl: "The Fishes of Illinois." Natural History Survey of Illinois, Vol. III: p. 232. Danville, 1908.

Dr. R. E. Coker[10] (1917) discusses the history of *Elassoma* and also gives a description of the species and its habits as observed in aquaria. He include a general description of the natural habitat of *E. zonatum* at Mound, Louisiana. The food habits of this species are mentioned with the question raised as to its probable value as an agent in mosquito larval control, in as much as he observed that it fed on entomostracans and mosquito larvae in aquaria. The hardiness of this little fish is indicated by the fact that seventy-five of them remained alive four days in a ten gallon milk can on an extended railroad trip. Dr. Coker used as an illustration the first published drawing of *E. zonatum.*

W. A. Poyser[11] (1919), an aquarist, describes the color patterns of male and female *E. zonatum* as he observed them in his aquarium. He mentions rapid changes in color patterns and in density of pigmentation which he understands as merely accompanying the spawning act. Observations in connection with the present study show that as the breeding season approaches the male and female become bluish black and pallid green, respectively, and remain so throughout the height of the breeding season which may last several weeks. As this season comes to its end the pigmentation gradually returns to normal, at which time the male and female again become hardly distinguishable by their color patterns.

Poyser accurately describes the spawning act, after having observed this twice in his aquarium. The eggs were laid, as he notes, at distances of seven and eleven inches from the bottom, fertilized as extruded, and sank to the floor of the aquarium, where they remained possibly protected from enemies by the male. No nest was prepared for the eggs.

ENVIRONMENT

In the vicinity of Mound, *Elassoma zonatum* was taken in only one small water system, which possessed a distinctive association of environmental features.

This habitat is Cypress Bayou (fig. 1), a typical winding bayou and "wild" except at a few road-crossings. It extends through several miles of plantation and wooded country, its size and distribution fluctuating generally with the seasons of the year, since its sources of supply, seepage and rainfall, vary usually according to season. The bayou at one end meets the levee of the Mississippi River from which it derives its seepage water, and inasmuch as the river is usually at its highest stage during the late winter and spring months, the seepage is therefore greatest at that time. Rainfall, the other source, averages for this locality about fifty inches annually, with the greater part coming between October of one year and May of the next. As a result of the coincidence of the factors of supply, the bayou surface with all its ramifications, consisting of ditches and cross-bayous, is very much more extensive during the spring than at any other time. As the summer approaches and the sources of supply diminish, there is a consequent decrease in surface area and depth which continues until the following October. Even though much of the bayou dries, there always remains a considerable portion which at the lowest water stage measures at least five feet in depth.

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[10] Coker, Robert E.: "The Pigmy Sunfishes." Aquatic Life, Vol. III, No. 2, October, pp. 22–24. Philadelphia, 1917.

[11] Poyser, W. A.: "Notes on the Breeding Habits of the Pigmy Sunfish." Aquatic Life, Vol. IV, No. 5, pp. 65–69. Philadelphia, January, 1919.

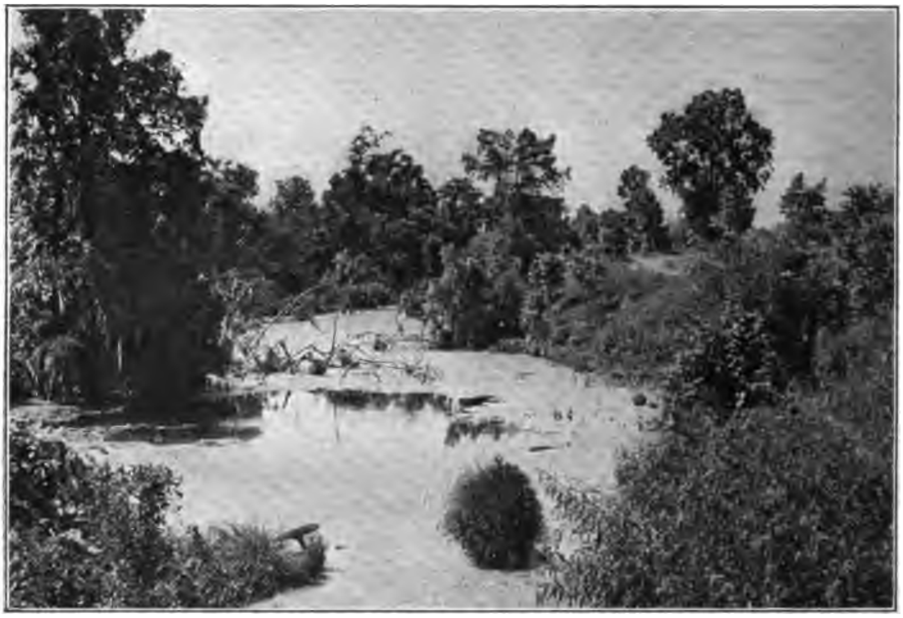

FIG. 1. Cypress Bayou, Mound, Louisiana; habitat of pigmy sunfish. Note the heavy mat of surface vegetation.

This section of the bayou which persists possesses to the most marked degree the environmental features which furnish the typical habitat of the pigmy sunfish. In this connection it is worthy of note that in all the many routine collections made for four years in certain ramifications and continuations of the bayou where the particular vegetative environmental features of the *Elassoma* habitat do not obtain, there has never been a single specimen of this species.

The outstanding floral characteristics of the *Elassoma* habitat at Mound are a heavy surface mat made up of *Lemna, Spirodela, Wolffia,* and *Azolla* in combinations varying seasonally, and beneath this mat a flourishing growth of *Ceratophyllum*. In the marginal waters where the surface growth is occasionally broken, filamentous algae are commonly found. From the annual deaths of the surface plants, resulting layers of decaying vegetation have covered the original bottom of delta mud to a considerable depth.

Co-habitant with *Elassoma* accidentally occurs *Gambusia,* which seeks out occasional open spots in the thick surface mat. *Fundulus henshalli, Amiatus calvus, Lepomis cyanellus,* and *Abramis chrysoleucas* are found also, but in very limited numbers. Early in the summer as the water depth decreases and the submerged vegetation is proportionately concentrated, the very physical nature of the *Elassoma* habitat makes it unsuitable for larger fish. In early spring during high water several other species have been found in this particular section of Cypress Bayou, some of them apparently breeding in these waters. Subsequent collections, however, reveal strikingly few individuals that might have come from these broods, a finding which demonstrates the unfavorable character of the *Elassoma* habitat for larger fish. Of the 351 fish taken in this portion of the bayou in the systematic biweekly collections of 1918 as a part of the mosquito larval control study, 339 or 97 percent were *Elassoma zonatum.* The nice adaptation of this species to its environment with the nearly total exclusion of other fish perhaps predacious on it very much enhances its possibility of survival.

The insect fauna of this particular habitat consists of the common aquatic forms, including representatives of the following: Belostomidae, Odonata, Dytiscidae, Notonectidae, Nepidae, and several dipterous families, especially the Stratiomyiidae and Chironomidae. Of these the Belostomidae and Odonata nymphs have been observed to be predators of the pigmy sunfish. Possibly others of the above list are likewise enemies of *Elassoma.*

In other sections of Cypress Bayou, representing entirely different associations of vegetative environmental features, both the insect and fish fauna stand in marked contrast to that discussed above. The number of species of fish and their relative frequency vary remarkably in different portions of the same bayou, and another bayou at not more than one half mile's distance has a fish fauna as characteristic as that of Cypress Bayou.

Description of Sexes.

The sexes in *Elassoma zonatum* are clearly differentiated, immediately before and during the breeding season, by the contrast in pattern and depth of pigmentation as observed in representatives of the two sexes taken at Mound (fig. 2). During three years of intermittent collecting in Cypress Bayou, no *Elassoma* had been taken either in a gravid condition or in a newly-hatched or very young stage until March 7, 1919, when several females whose abdominal parts were considerably distended were captured. Examination proved these fish to be gravid. That no gravid *Elassoma* had been taken in the bayou formerly was due to the fact that collections had never been made earlier than the latter part of April.

The female at the breeding period is of a decidedly light color compared to its appearance at other seasons. As it reaches a very ripe condition the vertical lateral bands, so characteristic of both sexes after the breeding season, almost entirely disappear, only a faint suggestion remaining. In life, the fish in general presents a light olive green appearance, there being a very noticeable reduction in lustre and contrast in the usually spotted and banded pigmentation. Even the pigmentation of the fins disappears. The pectoral, ventral, and anal fins are so colorless that when spread in their natural swimming position in the water they are transparent. The many small dorsal and caudal fin spots are very faint. The ordinary greenish metallic sheen of the opercle is lacking, while the head, with special reference to the lower jaw and isthmus, is entirely unspotted. The light pigmentation of the opercular region makes the bright red of the gills very evident through the translucent tissue of the opercular plates. The gravid female belly, swollen with ripe and ripening eggs, is rather long and oval in shape, quite different from the roundness of the gravid *Gambusia* belly. As the breeding season passes, the female color pattern darkens, the darkening beginning below the lateral line and extending upward until the usual banded condition similar to that of the male is reached.

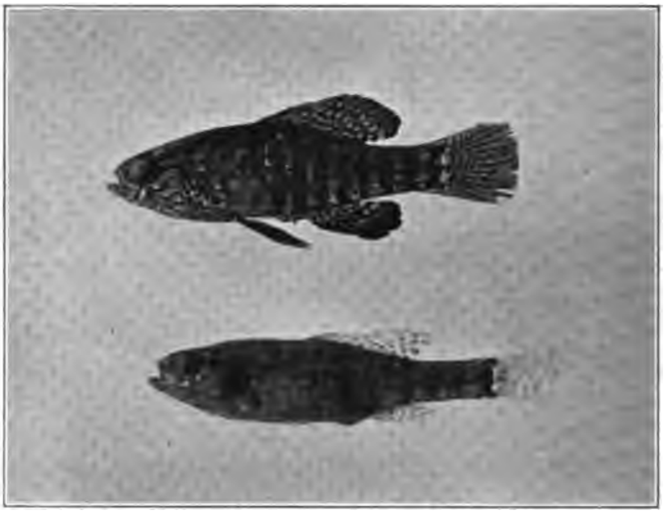

FIG. 2. Male (upper) and female *Elassoma zonatum* at the breeding season, × 7/4.

Of the 273 gravid *Elassoma* females taken during the breeding season of 1919 the largest measured 3.5 cm. from tip of head to the base of the caudal fin; the smallest, 1.8 cm. The modal length for all was 2.5 cm.

The male *Elassoma zonatum* in breeding season is readily distinguishable because of the increase of the pigmentation and its brilliant intensity. The male has a greater depth of body than the female and presents a very sturdy appearance, with a slightly larger head and heavier jaws. The general color of the male in life during the breeding season is a very dark bluish black, contrasting distinctly with its very lightly pigmented vertical bars. The lower jaws and isthmus are punctulate with many small black pigment spots, in strong contrast to the bluish white tissue in which they are set. The post-opercular region is nearly black, glistening with a lustrous metallic sheen of bluish green. In life the vertical bands of blackish pigment are clearly discernible as far posterior as the beginning of the anal fin, while the color reaches distinctly to about one half the distance below the lateral line where it blends with the black spotting of the compressed belly; in preservative the diffuse pigment which makes the lateral bars indistinct in life disappears and the several black stripes are plainly evident as far as the caudal fin. The black chromatophores appear in uniform bands on the opercles and isthmus, with regular rows of these dots in the region of the mouth. The spots in the dorsal region of the head are indistinct owing to the heavier diffused black pigmentation of that region. The fins of the males are all very dark, slightly larger than those of the female, and are finely punctulate with rows of black points. The ventral fins are longer and jet black, tapering to fine black tips. The spots are more numerous, darker, and more distinct in this sex.

Of the 131 males taken during the breeding season of 1919 the largest was 3.0 cm. in length; the smallest was 1.8 cm. The modal size for all was 2.4 cm.

In seven collections taken on different days in March, 1919, there were obtained 404 *E. zonatum*. Of these, 273 or 67.5 percent were females; 131 or 32.5 percent were males. This indicates that in nature the numerical relation of male to female is approximately one to two.

In all descriptions of *E. zonatum* which have been at our command special mention is given of a black scapular blotch; yet only 3 of 128 adults examined from one collection in April, 1919, had this type color pattern distinctly evident. These observations indicate the variability of the species as regards this character and discredit its value as a species-determining mark. The large majority of the fish observed showed only a slight broadening and darkening of the first, and occasionally of the first and second pigmented vertical bars posterior to the gill openings.

Breeding Habits

The breeding season for the pigmy sunfish begins in northern Louisiana about the middle of March. The first larvae of this species were taken on March 25th and the largest and most developed of these showed complete yolk absorption. This would indicate, from data already collected on the larval growth of *E. zonatum* and hereafter noted, that the eggs from which these fry hatched were laid at least by March 15th. The number of eggs laid by a female may be indicated by the table below. The figures give the number of ova taken from preserved gravid females captured near the beginning of the breeding period, March 25th. The ova thus studied would have been laid later in the season.

MARCH 25, 1919

Number of Female *Elassoma zonatum*	Number of Eggs Present
2.25 cm.	96 eggs.
2.35 "	325 "
2.4 "	175 "
2.6 "	310 "
2.65 "	260 "
2.9 "	500 "
3.2 "	575 "
3.5 "	970 "

Some of the above recorded fish may have released a small number of their eggs, and this doubtless accounts for any disparity in the general relation between size of female and number of ova.

The following tabulation was made of ova counted from fish taken April 25th, when by far the greater part of spawning had already occurred. The fish examined must have been rather late in ripening. Comparison of the number of ova present on the two dates, however, indicates that spawning is intermittent throughout the extent of the breeding season.

APRIL 25, 1919

Length of Female *Elassoma zonatum*	Number of Eggs Present
2.45 cm.	145 eggs.
2.6 "	236 "
2.6 "	150 "
2.5 "	200 "

The eggs are laid in quantities of forty to sixty in places protected by submerged vegetation. They are found scattered and covered with tiny bits of plant débris and silt. Occasionally some developing eggs were taken from among the strands of *Ceratophyllum* which had probably obstructed the falling of the eggs from the mother fish to the bottom. The ova require no care, as many artificially impregnated eggs that were left without attention in pans both in the natural habitat and in the laboratory showed normal development.

The spawning is repeated as a new batch of ova becomes mature, at intervals of approximately a week's time. All females taken during March were heavily gravid, about ten percent. of these carrying ripe spawn; while apparently all male fish were ripe, as fertilization occurred in all eggs where artificial impregnation was attempted. The water from which these fish were taken was somewhat warmer than in other parts of the bayou owing to the fact that recent heavy rains had swept away the surface mat of vegetation from this particular collecting spot. In parts of the bayou where the surface mat remained intact the water registered 57° F. at all times during collecting; while at the above mentioned clear space, where the sun could beat directly into the water with no obstructing vegetation, the temperature varied between 62° and 68° F. No ripe females were taken from the colder waters, and apparently the temperature was the determining factor that led the ripe fish to seek the open-surfaced area. The eggs are laid at a depth of from six inches to two feet, judging from the locations from which they were collected in our plankton nets.

That *Elassoma zonatum* after breeding seeks a different location, doubtless in deeper or cooler water, is indicated forcibly by the fact that on April 7th, in two hauls of a twelve-foot minnow seine, 128 adult *Elassoma* were taken, while on the 25th of April, in three hauls, only the four females above recorded and two adult males were obtained. This probable migration of *E. zonatum* after spawning is further borne out by the fact that in the biweekly collections of 1918 at this collecting ground not a single adult was captured that could have been from a brood hatched previous to the spring of 1918.

The eggs are spherical and measure .5 mm. in diameter. They are orange colored, semi-opaque, and contain one large oil globule measuring .15 mm. in diameter and many appreciably smaller ones. The large oil globule persists throughout the entire embryonic and larval stages until the yolk is absorbed. The eggs are demersal and slightly glutinous, as is evidenced by the fact that they occasionally cling to submerged vegetation. Often temporary concavities are observed in the ova, the result of mutual compression as they lie in the ovary prior to spawning. The ova water-harden quickly, the egg membrane measuring .2 mm. in diameter. This tissue is especially tough, an adaptation to the physical surroundings during the embryonic development of the egg. The ova can be stripped or cut from the ripe female *Elassoma* and readily fertilized by placing them in a receptacle with the macerated testes of a male. The incubation period of *Elassoma* eggs at 65° is approximately seven days.

EMBRYOLOGY

Immediately after impregnation the relatively small amount of protoplasm of the egg collects in a lenticular cap-like mass, the blastodisc. This is formed in about an hour and one half at 65°, and the several beginning stages of segmentation occur rapidly after the disc has developed until it encloses about one third the surface area of the ovum. At an early embryonic stage in which the outline of the broadening head and the rudiments of the tapering tail are just beginning to appear, slight pigmentation of the embryo is observed. The small chromatophores are not limited to the embryo proper but appear also on the extra-embryonic tissue surrounding the yolk. As growth continues the pigmentation is much more evident. On the sixth day when the embryo is nearly ready to hatch, the pigmentation extends over the entire body and the tissue about the yolk. The tail is wrapped closely about the yolk overlapping the lower head region.

LARVAL DEVELOPMENT

At the period of hatching the small larva measuring 2.7 mm. long wriggles actively forth from the protecting membrane. The larva remains quiet for the most part resting on its side on the bottom but giving occasional spasmodic swimming movements. From the beginning, as in the adult, the swimming is occasional but very swift. As the larvae develop they daily become more active.

The larva at birth is of a light straw color. The tissue is so transparent that the entire circulation can be easily observed. The newly-born fish is well pigmented, especially on the head and along the dorso-lateral region. The pigmentation extends noticeably down over the unabsorbed yolk-sac. There are several spots of yellow pigment distributed along the dorsal line and much diffuse yellow pigment on the frontal region.

Larval development is slow and for the first three or four days the noticeable developments include only a slight diminution of the yolk-sac, a little stronger black pigmentation, and thorough diffusion of all yellow chromatophores. The larva grows perhaps a millimeter in this period. During the fifth and sixth days the black pigmentation increases markedly on the upper yolk-sac. On the eighth and ninth days the jaws of the fish become quite distinct and the first evident approach toward fin differentiation is noticed. A typical larva at this stage measures slightly over 4 mm. On the fifteenth day the larva has taken on approximately the appearance of the adult. The jaws are fully formed, the yolk-sac absorbed, and the dark pigment somewhat diffused, giving the young fish nearly the likeness of the adult except for the lack of the pigmented striped color pattern of the fins and of the body. At this stage the little fish begins eating, taking bits of débris. It has been observed, however, that the stomach contents of several larval *Elassoma zonatum,* so young that their fins were not yet differentiated, consisted of small cladocerans. During the larval stages the fish is very hardy and has withstood in the laboratory changes of temperature of at least twenty degrees in the course of ten hours with no apparent ill effects. When the larva attains a length of 8.5 mm. it begins to show evidence of the presence of the vertical lateral bands typical of the adult.

GROWTH

During the period from May, 1918, to April, 1919, much information on the growth of the pigmy sunfish was collected. Within this time a total of 743 fish were taken in thirteen collections. Each collection had a sufficiently large number of *Elassoma* from which a fair modal length could be obtained. Each fish was measured and recorded and the modal length for all *Elassoma* in each collection was noted. From these data it is possible to construct a graph, figure 3, which very plainly indicates the growth of the little fish. It is suggested from this graph that the pigmy sunfish reaches its adult size and becomes sexually mature before it is a year old and, as our observations show and the graph indicates, at this age the fish will have produced a new brood.

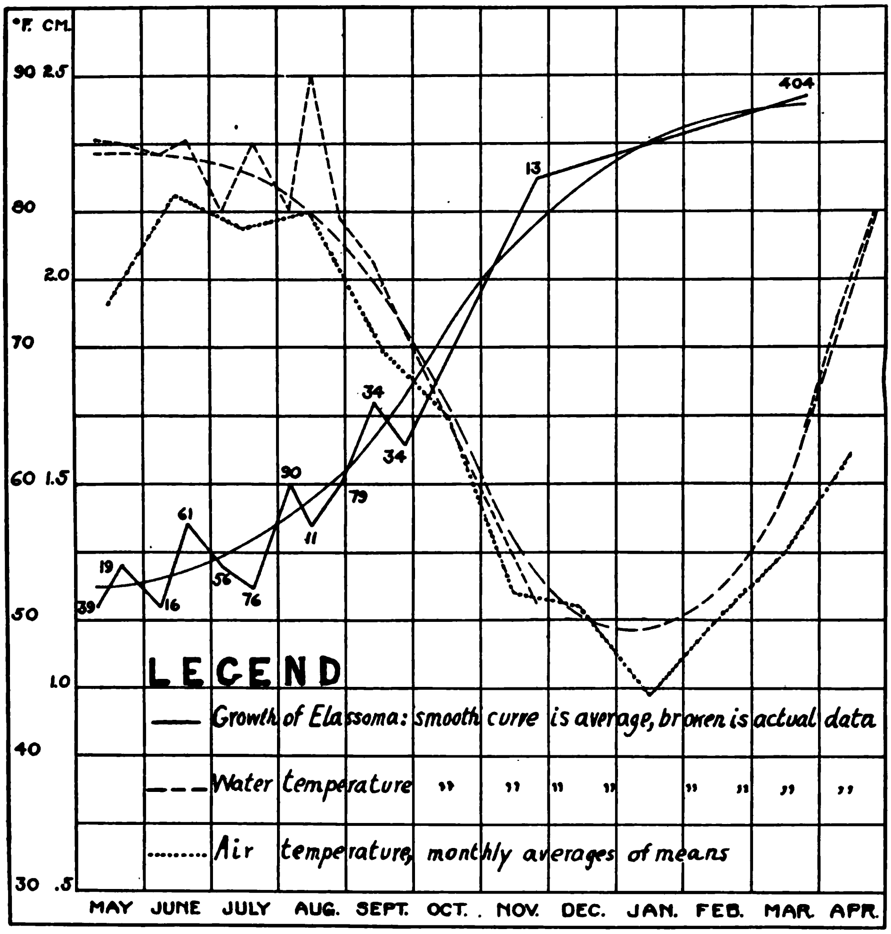

FIG. 3. The relation of the growth of *Elassoma zonatum* to season and temperature, for 1918.

The higher temperature which prevails during the summer months is of considerable significance in the study of *Elassoma* and, indeed, of all fish growth. First, it speeds up all physiological processes of the fish; simultaneously it quickens the photosynthesis of all plants—in this case especially *Ceratophyllum*—and the increased oxygen thus released by plant growth, in turn, serves to make the pool capable of supporting a larger number of oxygen-consuming forms—an automatic natural provision of a more healthful medium for fish life, plant life, and that of the smaller food organisms. In a word, the higher temperature means more fish food, more efficiency in its utilization, and a greater capacity for the pool in supporting fish life.

It is noticeable, also, in the graph that the temperature of the water, the medium in which all changes in plant and animal life occur to affect fish, varies almost regularly throughout the year with the changes in air temperature as indicated by the monthly average mean temperatures. Water temperatures, as indicated in the graph, were plotted by computing the mean between the temperature at the maximum depth and that at the surface.

The comparative straightening of the mean growth curve during the period from November to March of the succeeding year suggests the lowering in rate of metabolism during the winter months common to all cold-blooded animals, as caused by and coincident with the decrease in temperature of the water medium. Not only does this lowering of temperature thus influence the growth of the fish directly, but also indirectly through its effect upon the maturing, reproduction, and consequent abundance of those organisms which serve as fish food.

Realizing that during the summer and fall of 1918 Cypress Bayou had held a minimum of water, due to continued drought, and surmising that the relatively higher temperature of the water necessarily resulting from this drought might have had some effect on the growth of *Elassoma,* it was decided, in view of the fact that the data could be collected simultaneously with other material, that further similar observations on growth should be made during 1919. Fortunately the spring, summer, and fall of 1919 were of about normal rainfall and temperature, thus giving much data that might be well contrasted with the 1918 observations. These 1919 data gave a curve the general direction and shape of which is the same as that of 1918; however, it is about .2 cm. behind the 1918 curve at any chosen period of the year. This comparative tardiness in the growth of 1919 is due probably to the cooling effect that heavy rains and consequent greater depth had on the water in which *Elassoma* thrived. The concavity in the curve, though not characteristic of typical fish growth, seems to be normal for the development of *Elassoma* to full size.

Among the biweekly collections at the *Elassoma* habitat, beginning May 9, 1918, no adult pigmy sunfish over two centimeters long were taken until in November. All the catches were plainly of fish of the 1918 spring hatch.

It is remarkable that among the 267 *E. zonatum* taken before July 18th, there never appeared an adult, *i.e.*, one that had been sexually mature in the spring. It may be that the adults after producing their brood seek such deep and inaccessible waters that they were not obtained in the biweekly collections, although no information on this point is at present available. This seems to be borne out, however, from a study of the scales of certain of the largest fish collected during the early winter and spring. The scales of several of these fish indicated that they were about to complete their second year of life. The largest male taken in this study, 3.4 cm. in length, was in its third year.

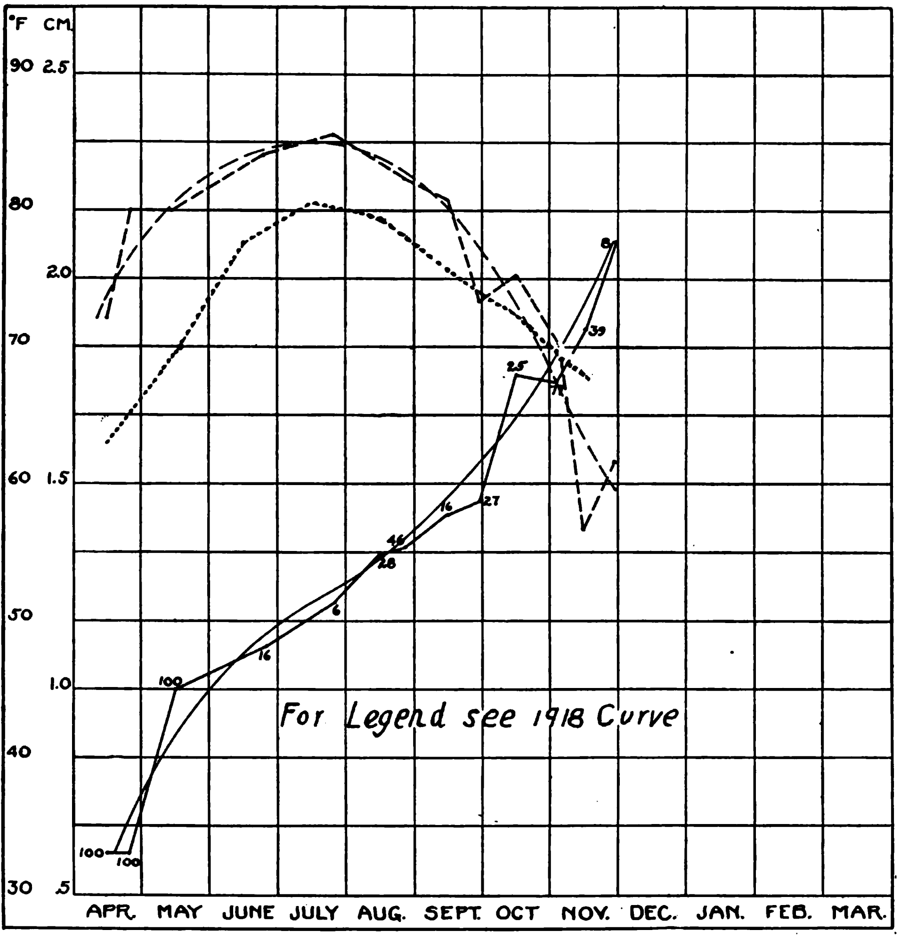

FIG. 4. The relation of the growth of *Elassoma zonatum* to season and temperature, for 1919.

STOMACH CONTENTS OF ELASSOMA ZONATUM

(Estimated Volumetric Percentage of Different Foods)

Period during which collected	No. of fish examined	Length in cm.	Crustaceans					Insects							Mollusks (Univalve)	Plants (Algal spores)
			Copepods	Cladocera	Ostracoda	Malacostraca	Total Crustacea	Chironomidae L. & P.	Stratiomyidae	Dipterous undetermined	Coleoptera	Odonata	nsecta undetermined	Total Insecta		
May 9, to Nov. 29, 1918.....	46	1.1 to 2.9	27.2	27.5	4.2	2.8	61.7	32.2	2.1	.2	.9	.8	2.0	38.2	0	.8
Mar. 7, to Mar. 31, 1918.....	26	2.3 to 3.25	25.0	35.0	10.8	7.7	78.5	0.	5.2	1.8	.0	.0	1.1	8.1	10.9	2.1
May, 1918 to Apr., 1919.....	72	1.1 to 3.25	25.8	29.8	6.6	4.5	66.7	20.5	3.2	.88	.62	.52	1.8	27.4	3.9	1.3

Food

A few fish of each of the biweekly collections of 1918, constituting in all 46 individuals, and 26 of the spawning adults taken in March, 1919, were examined to ascertain the character of food taken by *Elassoma* in nature. Determinations of the animal and plant life found in each stomach were made, and an approximate volumetric percentage of the different organisms present was recorded. These are herewith summarized.

From examination of the foregoing figures it will be noted that the small crustaceans constitute the major part of *Elassoma* food at all ages of the fish from two months through maturity. The aquatic larvae and pupae of several dipterous families, especially *Chironomidae,* are next in quantity. That there was only a small percentage of insect food in the adults' stomachs at breeding time is probably due to the fact that the insect fauna may have been less abundant at that time and, also, that snail eggs were hatching in great numbers on the strands of the submerged *Ceratophyllum.* It will be noted that these univalve mollusks constitute a tenth of the breeding *Elassoma* food.

It is worthy of notice also that vegetation makes up a negligibly small percentage of *Elassoma* food at all seasons of the year. The only plant forms found in the seventy-two fish examined were algal spores, probably motile or accidentally ingested with other food. It is also noteworthy that no fish of any kind was found in any of the stomach contents. This fact is a fair indication that this species is neither cannibalistic in nature nor predacious on other fish forms, especially since there were thousands of larval pigmy sunfish in the collecting place that doubtless made themselves noticeable by their spasmodic swimmings. It is hardly reasonable to think that the pigmy sunfish is predacious on *Gambusia* to any appreciable extent, even if the tendency were toward this, for it would be physically impossible for an *Elassoma* to devour a *Gambusia* unless the latter had lately been born. It is a significant fact in this connection that the natural habitat of *Elassoma* is such that *Gambusia* is absent therefrom, especially because of the latter's choice of open water spots unprotected from the sun. The two species would not be rivals for the same environmental area.

From the very nature of the food of *Elassoma,* in that it consists almost entirely of actively swimming or wriggling organisms—cladocerans, copepods, and chironomid larvae and pupae—it is very probable that this fish could be a valuable agent in mosquito larval control, if it thrived in waters where mosquito larvae were abundant. In the *Elassoma* habitat at Mound a heavy surface mat of vegetation apparently precludes almost all mosquito breeding with the exception of that of one species of *Culex* which is commonly found in such pools. In spring, however, before this mat has become thickly grown and while there still remain many small open spots suitable for mosquito deposition, these fish may be more or less of a natural control on anopheline mosquitoes.

ENEMIES

Elassoma in its natural hatitat at Mound has few competitors. It is true that should this fish wander from its home of thick submerged plant growth, it would quickly find numerous enemies among the fish. In its own environment, however, fish enemies are very few. Only occasional individuals of *Amiatus* work their way into the heavy *Ceratophyllum*. In its habitat snakes or fish-eating birds can do *Elassoma* a minimum of harm. Large water beetles, bugs, and Odonta nymphs are probably the only forms which the pigmy sunfish has to contend with.

SUMMARY

The occurrence of *Elassoma zonatum* appears to be closely co-related with a distinctive combination of environmental features. At Mound, Louisiana, it was found only in a typical "wild" bayou heavily grown with submerged *Ceratophyllum* and a thick surface mat of *Lemna, Wolffia,* and *Spirodela.* The nice adaptation of the species to its environment, and nearly total exclusion of other fish, much enhance its possibility of survival. It is hardy, both in its larval and adult stages.

The contrasting color patterns and the differing pigmentation of male and female *E. zonatum* immediately before and during the breeding season serve as means of distinguishing the sexes.

The breeding season of *E. zonatum* in northern Louisiana begins about the middle of March and lasts until about the first of May. The temperature of the water appears to be the factor determining the place where the eggs are laid. Under the mat of vegetation the water was 57° F., while the open water varied from 62° to 68° F.; gravid females and eggs were taken only in the warmer water.

An average-sized female may lay three hundred or more eggs, which are dropped at intervals of several days in lots of from forty to sixty. No nest is prepared. The eggs pass through a normal embryonic development and hatch in approximately seven days. After breeding, the fish seeks cooler and deeper water.

Growth is rapid in the larval and young stages. Curves of temperature (air and water) and rate of growth show that growth is more rapid when the water is warm and is retarded as the adult stage is reached and the water becomes cooler in November and December. The fish produces its first offspring when just a year old.

The food of *E. zonatum* consists principally of small crustaceans, larval and pupal aquatic insects, and small mollusks in some seasons. The size and habitat of *E. zonatum,* and the very nature of its food, make it very probable that under some conditions this species may be more or less of a natural control of *Anopheles* mosquitoes.

The larger aquatic insect forms, both larval and adult, rather than fishes, are probably the most destructive enemies of *E. zonatum* in its native habitat.

SOME BOTANICAL AND ENVIRONMENTAL ASPECTS OF HAWAII

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Few regions anywhere are more interesting botanically than the Hawaiian Islands.

Owing to their extreme isolation, separated by 2,000 miles of ocean from the nearest land mass of any size, there is an extremely high percentage of endemic species, many of them remarkably specialized, testifying to the long period during which evolution has been going on with little disturbance from outside.

Except for the almost uniformly volcanic nature of the soils, which has no doubt been a factor in the evolution of the flora, the conditions are extremely varied. Owing to the great height of some of the mountains, which in the two great cones on the island of Hawaii, Mauna Kea and Mauna Loa, rise to nearly 14,000 feet, and overtop all the mountains of Polynesia and Australasia, there is a corresponding range of temperatures, from the tropical heat of the lowlands, to regions of almost perpetual snow. The variation in precipitation is also extraordinary, ranging between an annual rainfall of 400–500 inches in extreme cases,[1] to less than 20 inches in some of the dry leeward districts. These remarkable differences of elevation, temperature and moisture occurring within a quite small area afford the botanist unusual facilities for investigating a wealth of extraordinarily interesting problems in plant evolution.

The writer has made several visits to Hawaii, the last in the summer of 1919. Two years before, a trip was made for the purpose of collecting Hepaticae for comparison with certain East Indian species which indicate an interesting similarity in the hepatic floras of the two regions. This led to a somewhat critical study of the Hawaiian flora as a whole, which revealed an unexpected and most remarkable affinity with that of the Australasian and Indo-Malayan regions. So many were the correspondences that they led inevitably to the conclusion that these could only be explained satisfactorily by assuming the existence of some ancient land connections which have disappeared in a great general subsidence of the whole Polynesian area.

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[1] A five years' record on Mt. Waileale, Kauai, showed an average annual precipitation of a little over 500 inches. See Science for November 23, 1917, pp. 511–512.

The results of these studies have been published already[2] and will not be enlarged upon here.

The Hawaiian Archipelago consists of a chain of islands extending from northwest to southeast, between lat. 18° 55′ and 21° 15′. Its total area is 6,454 sq. mi., of which nearly two thirds is comprised in the southernmost island, Hawaii. To the N.W. a long series of small islets or reefs extends for about 18 degrees. All the islands, except for the coral reefs are volcanic; but at present the volcanic activity is restricted to the island of Hawaii, which has two enormous active craters, where the process of mountain building can be seen at any time. Volcanic outbursts of spectacular proportions have been a feature of the past two years, and last September a large lava flow burst out of the flank of Mauna Loa, and finally reached the sea, where it built out a promontory of considerable size.

In the older islands all activity ceased long ago, and the disintegration of the volcanic soils is complete; but in Hawaii, and to a lesser degree elsewhere, there are large expanses of bare lava, nearly or quite destitute of vegetation. The volcanic activity has evidently developed along a rift beginning at the northern end of the present chain of islands, and has proceeded southward, where it is now seen in the active craters of Hawaii.

There is strong evidence that all the large islands were once united into a single much larger land-mass, which through subsidence has gradually segregated the islands as they now exist. The northernmost island, Kauai, was the first to be detached, this being indicated, both by the deep and broad channel between it and its neighbor to the south, Oahu, and by the very highly specialized nature of its flora. The proportion of endemic species is higher in Kauai than in any other island, although it is one of the smallest.

The topography of the islands, especially the older ones, is excessively rugged. The windward districts are drenched with torrential rains, deposited by the moisture-laden North East trades. The resulting erosion has made innumerable deep and precipitous canyons, whose walls are often almost perpendicular. These vertical cliffs, "palis," whose brinks are often concealed by dense vegetation, make it very dangerous to wander about without a reliable guide.

In the older islands the mountains are much worn down and the highest summits are only 4,000–5,000 feet in elevation. The great cones of Maui and Hawaii, the most recent of the islands, however, are much higher, Haleakala on Maui being about 10,000 feet high, and Mauna Loa and Mauna Kea on Hawaii, nearly 4,000 feet higher.

On these lofty islands nearly all the moisture is precipitated on the windward (N.E.) side, while in the less elevated islands, much of the moisture is carried over the summits of the mountains and precipitated on the leeward side. This is seen very clearly back of Honolulu, where the heaviest precipitation is at the head of the valleys on the leeward side of the mountains. The leeward shores are relatively dry, and even arid in many places, so that the contrast between the scant vegetation of the sun-baked lee shores and the rank vegetation of the upland bogs and rain forest is sufficiently striking.

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[2] "The Derivation of the Flora of Hawaii." Leland Stanford Junior University Publications, 1919.

Little is left of the indigenous vegetation of the lowlands, except in some of the most barren districts—and even in these, exotic species have to a great extent driven out the native. Thus in some of the waste rocky districts near Honolulu, prickly pear cactus has taken almost complete possession. Practically all of the arable land of the lower levels is under cultivation, the huge plantations of cane and pineapples monopolizing most of the land not occupied by rice-fields, taro patches and home gardens. Most of the conspicuous trees, shrubs and weeds are introduced, and give to the casual observer an entirely erroneous impression of the native flora. In the neighborhood of Honolulu, for instance, the two most conspicuous trees are the Algarosa (*Prosopis* sp.) and Iron wood (*Casuarina equisetifolia*). Both of these are of comparatively recent introduction, but have become completely naturalized and have all the aspect of being indigenous. It is highly probable, also, that the cocoanut palms were introduced by the natives when they invaded the islands. Many foreign weeds have become thoroughly established, and in the hills back of Honolulu almost impenetrable thickets of Guavas and Lantana have taken possession, while in the dryest places the prickly pear and thorny acacias thrive. In the moister parts of the islands some very attractive exotics have become naturalized. Wild ginger (*Hedychium coronarium*), *Canna indica, Clerodendron* sp., Ipomoeas, and passion flowers are common along the roadsides and in the woods about Hilo and in the rainy valleys back of Honolulu, and elsewhere.

The strand flora includes such widespread types as *Hibiscus tiliaceus, Ipomoea pes-caprae, Scaevola frutescens,* Pandanus, and Calophyllum,—all types familiar to anyone acquainted with the strand vegetation of the Eastern tropics and the South Seas; but the strand flora as a whole is very poor when compared with the latter regions. There is a considerable number of endemic strand plants, but these are, as a rule, not very common, and are often very much restricted in their range.

While little is left of the lowland native vegetation, except for the strand flora, the forests, where they have not been destroyed—intentionally or otherwise—harbor many very peculiar indigenous trees and shrubs, as well as a rich flora of ferns, liverworts, mosses, lichens and fungi. Herbaceous flowering plants are relatively scarce.

The predominant trees of the lower forest are two—the "Kukui" (*Aleurites Moluccana*), and the "Ohia" or mountain apple (*Eugenia Malaccensis*). The former is very conspicuous on account of its pale silvery green leaves, which contrast strongly with the dark green foliage of the other forest trees. Its oily seeds were formerly much used by the natives. The showy red fruits of the Ohia are very refreshing and are relished by the white inhabitants as well as the natives. As both the Kukui and Ohia are of considerable economic value, and as they are common in the South Pacific regions, it may well be that their seeds were brought to Hawaii by some of the early native immigrants.

The upper forest zone—3,000–4,000 feet, especially on the windward side of the islands, is a pronounced rain forest, with dense undergrowth and many epiphytes. These include numerous ferns, among them several species of filmy ferns, the big bird's nest fern (*Asplenium nidus*)—*Ophioglossum pendulum,* several species of Lycopodium and various other forms. The lianas are not abundant, the most conspicuous being a Freycinetia, which, however, is more abundant at lower elevations.

The predominant tree of all the higher forest is *Metrosideros polymorpha,* which is extremely adaptable, as it occurs at all altitudes from near sea-level to more than 4,000 feet in elevation. The showy red flowers are produced in great profusion and are assiduously visited by some of the honey-sucking birds belonging to the peculiar Hawaiian family Drepanididae.

An examination of the trees and shrubs of the lower forest zone will show that many of the genera are characteristic of the South Pacific regions, Australasia, and Indo-Malaya. Pandanus and Freycinetia represent the Pandanaceae, quite absent from America, and many others are members of extra-American genera. Among these are Pittosporum, Gardenia, Coprosma, Metrosideros, Santalum, Cyrtandra, Dracaena and others. This affinity of the flora with the regions to the south is shown also by the Pteridophytes and Hepaticae.

The preponderance of Old World and Australasian genera, and the paucity of American types, is the most remarkable feature of the vegetation as a whole.

As in all tropical mountain forests ferns constitute a conspicuous part of the vegetation. Tree ferns of the genus Cibotium abound in all the rainforests, and are especially fine in the mountain forests of Hawaii. The peculiar Hawaiian genus Sadleria develops a short trunk, but is much inferior in size to Cibotium. The Marattiaceae are represented by a single species, *Marattia Douglasii.* There are several species of Ophioglossum, including the striking epiphytic *O. pendulum* and several species of Gleichenia are abundant. There is a single species of Schizaea, and several Hymenophyllaceae, in addition to a large number of Polypodiaceae.

There are no Gymnosperms, and several widespread tropical genera that one would expect to find are absent. Most noticeable perhaps is the absence of any native species of Ficus, one of the most widespread genera of trees. The Orchidaceae are very poorly represented, only three species being recorded from the Islands, and there are no Araceae that can with certainty be considered as truly indigenous.

There are a good many endemic genera, mostly trees and shrubs, belonging to several families. Among these are Platydesma (Rutaceae), Pterotropia and Cheirodendron (Araliaceae), Gouldia and Straussia (Rubiaceae), Raillardia, Hesperomannia (Caupositae). Perhaps the most interesting family, from the standpoint of evolution, is the Lobeliaceae. This family has developed in a most remarkable way in Hawaii, and contains some of the most striking members of the flora. The genus Lobelia is represented by a number of species, but it is the two endemic genera, Clermontia and Cyanea which show the most remarkable developments. Some of these are tree-like, the largest 10 metres or more in height, the tall stems sometimes unbranched, and terminating in a palm-like crown of huge lanceolate leaves, below which are clusters of curious flowers.

The only indigenous palms belong to the genus Pritchardia. These are small or moderate-sized fan palms, occurring on all the islands, but not in great numbers.

OAHU

The Island of Oahu, upon which is situated Honolulu, naturally has been most exhaustively studied botanically. The immediate vicinity of the city is entirely under cultivation, and practically nothing is left of the original vegetation. Back of the city, however, are several valleys indenting the low mountain range extending the greater part of the length of the island. At the heads of these valleys and above them, there still remains a considerable extent of forest, which harbors many of the interesting indigenous plants and gives a fairly good idea of the character of the original flora.

The main range of Oahu is low, scarcely exceeding 3,000 feet at its highest point, and the moisture-laden trade winds pass over the summit and deposit a large share of their moisture at the head of the valleys on the leeward side. There is a remarkable difference in rainfall between the head of these valleys, where it may reach 200 inches annually and the dry coastal district at their openings, only a few miles distant, where it may be less than one fourth as much.

Of the valleys back of Honolulu, one of the largest is Manoa, whose physiography and vegetation have been discussed at some length in a recent paper by McCaughey.[8] The lower part of the valley is now part of the city, and even before this was the case, the floor of the valley had been taken up by the gardens and plantations of the natives, so that the native vegetation has long since disappeared. The head of the valley, however, still harbors much of the original forest, although the lower levels have been so ravaged by cattle and the inroads of wood cutters, etc., that most of the forest has disappeared and a jungle of guavas, Lantana, and other introduced shrubs and weeds have pretty effectually driven out the original growths. One of the worst weeds is the Hilo grass (*Paspalum conjugatum*), which rapidly invades the least clearing in the forest and soon chokes out the ferns and other delicate plants which form the natural ground cover. The rank growth of the grass makes it impossible for most tree seeds to germinate, and the doom of the forest is sealed.

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[8] McCaughey, V. American Journal of Botany, 4: 561–603, December, 1917.

Where the lower forest still exists, it is composed largely of the Kukui (Aleurites) and Ohia (*Eugenia Malaccensis*) already referred to.

Above the Kukui zone is a region characterized by another important native tree, *Acacia Koa,* allied to the phyllode-bearing Australian species. Above the Koa zone is the rain-forest in which are found many of the characteristic native trees and shrubs, very largely endemic species. Among these are species of Antidesma, Cheirodendron, Eugenia, Ilex, Hesperomannia, Metrosideros, Osmanthus, Pelea, Pittosporum, Pritchardia, Santalum, Suttonia, Straussia, Clermontia, Coprosma, Cyanea, Hibiscus, and others.[4] In this rain forest there is a rich growth, also of ferns, liverworts, and mosses.

The gardens of Honolulu are famous for their display of tropical and subtropical vegetation. One may see there most of the gorgeous flowering trees, shrubs and climbers of the tropics as well as many varieties of tropical fruits. A specialty of the Honolulu gardens is the great variety of Hibiscus. The scarlet *H. rosa-sinensis* has been crossed with some of the handsome native species and the result is a wonderful variety of most beautiful forms. The garden planted by the late Dr. Hillebrand, author of the Flora of Hawaii, still exists and contains magnificent examples of many rare palms and other tropical trees, some of really gigantic size.[5]

KAUAI

The northernmost island, Kauai, is the richest of the islands in number of species, and in the percentage of endemics. It is also the most productive in proportion to its size, the fertile soil and abundant water giving it the popular name of the Garden Island. The greater part of the area is occupied by an elevated plateau about 4,000 feet high, rising in the center of the island to 5,000 feet in Mt. Waileale. The latter is, so far as records show, the rainiest spot in Hawaii, and certainly one of the wettest anywhere (see footnote 1). The region about Waileale is occupied by grassy bogs and swampy forests of scrubby trees, which are extremely difficult to traverse as the writer can testify. The open bogs are much like those of northern regions and harbor many temperate plants, such as *Drosera longifolia,* Sphagnum, species of Rubus, Vaccinium, Viola, Geranium, and various coarse grasses and sedges. This region is also characterized by a number of single representatives of genera which according to Hillebrand belong in the Antarctic regions, New Zealand, Falkland Islands, and the Southern Andes.[6]

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[4] For details see McCaughy, loc. cit.

[5] For a detailed account of the ornamental trees, the reader may refer to Prof. J. F. Rock's "Ornamental Trees of Hawaii (Honolulu, 1917).

One of the most conspicuous plants of the wettest rain forest, found in all the large islands at elevations of 3,000 to 4,000 feet, is *Gunnera petaloidea* Gaud., which suggests a particularly luxuriant rhubarb, the huge leaves being 3 to 4 feet across, or even more. The genus is best developed in New Zealand, but has representatives in Chile and one species in the Malay Archipelago, but is not known elsewhere in Polynesia.

MAUI

Maui, the second in size of the islands, consists of two parts, East and West Maui, connected by a low isthmus. These two parts are of different ages. West Maui is evidently much older, and it is thought may have been connected, formerly, with the Kohala Mountains in N. E. Hawaii. The summit is almost 6,000 feet in height, and is occupied by bogs, said to be much like those in Kauai; and there are deep gorges on the windward side cut out by streams of considerable size.

East Maui is made up entirely of the gigantic volcanic mass of Haleakala, 10,000 feet high, with a huge extinct crater over twenty miles in circumference, and 2,000 to 3,000 feet in depth. Although there is no record of eruptions, there is every evidence that activity has ceased only in relatively recent times, and the lava flows within the crater look as if they had just been formed.

Much of the forest on the dryer slopes of Haleakala has been entirely destroyed by cattle, but in the wetter districts there are still dense rainforests of the most pronounced type. These are best developed at about 4,000 feet elevation. Above this the precipitation is much less and the whole summit of Haleakala is decidedly arid.

HAWAII

From an ecological standpoint, Hawaii, much the largest of the islands, is perhaps most interesting, although it is much poorer in number of species than the older islands. A small district in the northeast corner is occupied by the low range of the Kohala Mountains, very much older than the rest of the island, and probably once connected with West Maui. The greater part of Hawaii is composed of three large volcanoes, Mauna Loa, Mauna Kea, and Hualalai. The former is still in activity, and has two enormous craters, one of which, Kilauea, is familiar to all the tourists who visit Hawaii. The summit crater is difficult of access and is seldom visited. Owing to the presence of this great active volcano, such problems as the effects of volcanic eruptions upon vegetation, the invasion of recent lava flows by plants, and the establishment of new plant societies, and kindred problems, can be carried on in Hawaii as they can scarcely anywhere else. Owing to the great elevation of the mountains nearly all the moisture is precipitated on the windward side of the island, and much of the leeward or "kona" side is a desert of dead lava. Hilo, the principal town, is situated on the windward side, and the whole district is extremely wet, the annual rainfall in Hilo being not far from 200 inches. Being the most southerly of the islands, this great rainfall results in an extremely luxuriant vegetation and Hilo is decidedly the most tropical-looking place in all the territory.

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[6] F. Hillebrand: "Flora of the Hawaiian Islands," Introduction, p. xxiv.

Formerly covered with forest to the water's edge, the lower slopes of the mountains are now completely cleared, and up to 2,000 feet they are principally devoted to cane fields. Above this, owing largely to the ravages of cattle, the forests are rapidly disappearing.

The rain-forest is evidentry very quickly affected by any disturbance of the balance of species, and the invasion of cattle or other herbivorous animale not only destroys the native undergrowth, but allows the intrusion of weeds, especially the Hilo grass, which quickly destroys the ground cover of ferns and other delicate plants, and makes it impossible for the forest to perpetuate itself, both because the trees cannot long survive this exposure resulting from the destruction of the undergrowth, and because the conditions for germination of their seeds have been destroyed. Very soon the trees die, and what was a dense jungle becomes an open waste of grass and weeds, with the shabby remnants of a few tree ferns, and the stumps and skeletons of dead trees (an example of forest destruction along the road from Hilo to the volcano is described below).

The destruction wrought by grazing is seen on a large scale on the slopes of Haleakala in Maui, and on the Waimea plains of Hawaii. In some parts of the Islands, goats have run wild, and are the source of much damage to the vegetation.

The effects of erosion on the windward side of Hawaii are very remarkable. From the steamer approaching the shore there are visible the openings of deep valleys, cutting through the high cliffs which fall perpendicularly into the sea. Not infrequently the stream which has cut the gorge forms a cataract over a high cliff into the ocean.

Through the kindness of Dr. H. A. Lyon of Honolulu, the writer had an opportunity of collecting at the head of the largest of these gorges, Waipio Valley, which extends into the Kohala Mountains, the oldest formation of the Island.

The head of Waipio gorge divides into several branches, whose almost sheer walls fall straight to the floor of the canyon, 3,000 feet below. The cataracts falling over these vertical cliffs, except for their lesser volume, recall some of the falls of the Yosemite Valley. A narrow trail skirted the brink of this tremendous chasm, and above it rose a rocky wall, indented here and there with little caves, and covered thickly with a wonderful profusion of ferns, liverworts, and mosses, the liverworts in particular being extraordinarily abundant and luxuriant. Everything pointed to a tremendous rainfall, and we had a practical illustration in a succession of heavy showers which drenched us to the skin. At one place great cushions of Sphagnum were seen, an unusual sight in Hawaii, and beyond the gorge was an extensive nearly level boggy region, full of interesting plants, including a few specimens of a fan palm (*Pritchardia lanigera*). In this remote region very few introduced plants had got a foothold, the vegetation being almost entirely composed of truly indigenous species, among which were a number of interesting Lobeliaceae.

Very different was the aspect of the great Waimea plain, only a few miles from the Waipio gorge, and extending to the lower slopes of Mauna Kea. This region was formerly heavily forested but is now a treeless plain, the grazing ground for thousands of cattle.

The region about Hilo is very interesting botanically, although one has to go a long way to find the forest still standing. Owing to the great humidity, rain-forest types may be found near sea level, in gorges where remnants of the forest still remain. Filmy ferns, many liverworts, and species of trees and shrubs which usually grow at much higher elevations may be found. A remarkable instance was seen near Hilo. In 1881 a great lava flow almost reached the city, which was threatened with destruction. The great expanse of lava is still easily recognizable, although it is covered with the beginnings of a new forest. The roof of a large lava tunnel has broken through, forming a cave, open above, but well sheltered from the sun and wind. In this cave there is a luxuriant growth of ferns and liverworts, as well as some thrifty trees and shrubs, which have grown much better than their companions on the exposed lava above them.

Dr. Lyon pointed out a most interesting fact, viz., that practically all the plant colonists on the lava were strictly indigenous species. The introduced plants, like the weeds abounding along the roadside and in the cultivated land in the immediate vicinity, failed to obtain a foothold on the lava, while the indigenes seemed to find exactly the conditions they needed.

The most important element of the embryo forest is *Metrosideros polymorpha,* which quickly appears in Hawaii upon the recent lava flows. In the rain-forest, this tree most commonly begins as an epiphyte, especially upon tree-ferns, and often develops stilt-roots like those of many species of Ficus. As seems to be always the case in the colonizing of fresh volcanic soils, Pteridophytes play an important rôle. The characteristic fern, *Sadleria cyatheoides,* and species of Lycopodium and Psilotum, are among the early growths to appear; and a Vaccininum, with showy red and yellow berries, the "Ohelo" of the natives, is a common and conspicuous denizen of the lava.

A visit to the volcano was not without its melancholy aspects. When the writer made his first visit to this remarkable place in 1892 the greater part of the road from Hilo was through a dense unspoiled rain-forest. In some of the lower forest the undergrowth had been partly removed for the planting of coffee but otherwise the forest was left intact, and there was most interesting collecting within a short distance of Hilo. Now all the lower forest has disappeared to make way for cane, which covers all the available land. Most of the forest along the volcano road has either been cut down or has been so ravaged by cattle and the consequent encroachment of Hilo grass and other weeds, that very little of it is left. The last forlorn stragglers of the myriads of tree ferns that formerly lined the road, are slowly dying, exposed to the sun and wind, and the skeletons of dead trees rise from a waste of tangled weeds and grass.[7]

The country about the crater of Kilauea is decidedly interesting botanically. It is much dryer than Hilo and further on becomes very barren. Much of the region about the crater is covered with recent lava flows upon which a sparse vegetation has developed which gives a fair index as to the age of the different flows. Occasionally quite heavily wooded patches are seen, showing areas that were surrounded by the lava-flows but escaped destruction. These islands of older vegetation, "Kapukas" in the native tongue, are very interesting features of the region about the volcano.[8]

The remains of a magnificent forest of Koa (*Acacia Koa*) still exist not far from the volcano, but this has been used as pasture and invaded by Hilo grass, so that apparently seedlings cannot get a start, as nothing but mature trees can be found. Twenty-five years ago there was a fine undergrowth of tree-ferns and other native plants, but these have pretty much vanished and it will not be long before the forest has disappeared unless steps are taken to restore something like the original conditions.

Of the rain-forest below the crater, little is left in the vicinity of the volcano. A few small tracts have been enclosed—notably one belonging to Mr. W. M. Giffard of Honolulu, who kindly permitted the writer to collect there. These enclosed tracts show what the forest was in earlier days. Especially striking are the beautiful tree-ferns—*Cibotium Menziesii* and *C. Chamissoi*—which formerly abounded throughout the forest regions between Hilo and the volcano. A profusion of small ferns, as well as dense growths of liverworts and mosses cover the trunks and lower branches and even the leaves of the trees and shrubs.

An unusual and interesting little collection of plants was met with close to the active crater. Steam vents opening into a rift near the wall of the crater produced a small natural hot-house, where the heat and moisture had caused quite a luxuriant growth. The wall of the fissure, close to the steam vents, was covered with a thick, slimy coating of several species of Cyanophyceae, which displayed various bright tints. On the ground were several ferns and other plants, including an Ophioglossum, which has not been found elsewhere at this elevation, but occurs at sea level in the warm lowlands.

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[7] [This is a particularly good example of the influence of the "biological factor" of the environment. We have enough—and too many—cases of forest destruction in this country, but few in which the identical spot has been described both before and after the destruction occurred.—Ed.]

[8] For a fuller account of the flora of the volcano region see Rock, "The Indigenous trees of Hawaii." Pp. 27–33. Honolulu, 1913.

Comparatively few of the native plants produce showy flowers, although there are some of marked beauty, such as several species of Hibiscus with large white or yellow flowers. Some species of Lobelia and Scaevola are quite showy, and the scarlet flowers of Metrosideros and the leguminous climber, *Strongylodon lucidum,* beloved of the honey-sucking birds, are very conspicuous. Near the volcano these birds are quite common, and when perched near the scarlet flower clusters of the Metrosideros it is not easy to distinguish the red bird from the red flowers. Most of these birds have a long curved bill, which seems specially adapted to probing the curved tube of the Lobelias and the long curved keel of the Strongylodon.

The great preponderance of Southern Pacific and Asiatic types in the Hawaiian flora is very evident. The writer has treated this topic at some fifty extra-American genera are common to Hawaii and the regions of the South Pacific and Indo-Malaysia, while the number of strictly American genera occurring in Hawaii is only six. There are nearly forty extra-American species of Pteridophytes common to Hawaii and the Australasian-Indo-Malaysian area, while only two peculiarly American species are known from Hawaii. The Hepaticae show much the same relations.

The animal life of the Archipelago shows much the same correspondence with the faunas of the Southern hemisphere as is shown by the floras of the two regions.

Various explanations have been offered as to the origin of the Hawaiian plants, based on the assumption that the Archipelago has always been completely isolated, and is of purely volcanic origin, having been thrown up from great ocean depths. The nature of the flora of the Islands is scarcely to be reconciled with such a theory, since a large proportion of the plants, whose nearest reatives are in Australasia and the Malay Archipelago, possess no provision by which they could have survived the long journey over four or five thousand miles of ocean. A large number of these plants, including such delicate forms as the filmy ferns and many liverworts, inhabit the cool rain-forests, and one finds it difficult to conceive any means of transport length in two earlier papers,[9] and will not dwell upon it at length here. Over from distant New Zealand or the mountains of Java and New Guinea to the mountain forests of Hawaii which would enable the spores of these delicate plants to survive the exposure of such a journey.

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[9] Campbell, D. H.: "The Origin of the Hawaiian Flora." Memoirs of the Torrey Botanical Club, 17, 90–96–1918.

Loc. cit., 1919.

It is evident that most of the forms have been in the Islands for a very long time, as a great majority are endemic, although related to species or genera in other parts of the world. The extraordinary degree of endemism is scarcely equalled anywhere else, and points to a long period of isolation since the introduction of the ancestors of the present flora. This long isolation has resulted in a good many endemic genera, as well as species.

The small number of American types is remarkable, inasmuch as there are agencies which might be expected to bring to the Islands a good many plant immigrants. A considerable number of birds are regular migrants from the West Coast of America, and the prevailing trade winds are from the same direction. Moreover ocean currents frequently bring drift from the Northwest American shores. None of these agencies can be called in to account for the transfer of seeds from the remote regions to the South, whence it is certain most of the plant life of the Islands has been derived.

It seems necessary, therefore, to assume some ancient, more or less direct, land communication with the regions of the Southern Pacific. There is good evidence of extensive subsidence in the Hawaiian Archipelago which has resulted in the formation of the separate islands that now exist. This is most strikingly borne out by the flora of Kauai, which it is believed was first cut off. The flora of Kauai is not only the richest in number of species, but the species are most highly specialized and many are found exclusively in this island, indicating an early separation of the island from the other members of the Archipelago.

The island of Hawaii offers a great contrast to Kauai. Many times larger, it is for the most part made up of recent volcanic formations, a considerable part of which are still almost destitute of vegetation. The flora of this great Island, except in the small area occupied by the ancient Kohala range, is much less varied than that of the older islands, and comprises relatively few species, which are not found in the other islands.

A similar subsidence probably has occurred throughout Polynesia, and it is likely that at some remote period, perhaps in the early Tertiary, there existed one or more large land masses over what is now Polynesia, the existing islands being the summits of sunken mountain masses.[10]

It is known that the Malayan Archipelago was once united with the Asiatic mainland, and that the southern extremity of the American continent was connected in some fashion with New Zealand. The remarkable similarity between the floras of Hawaii and these southern land masses indicates, in the opinion of the writer, that the existing flora of Hawaii is in large part descended from types which were widespread over the great land areas which in Tertiary time, perhaps, connected Hawaii with the ancient continents of the South Pacific. These ancestral forms, in the course of ages have become much altered in many cases, but others have persisted with but little change. Presumably a good many forms have become extinct, and a considerable number of new ones have been introduced from outside. This is probably true of all the species which are allied to types from the Pacific Coast of North America. The time when the isolation of the Archipelago became complete must be largely conjectural, but to judge from the character of the fauna, it may well have been in the Mid-Tertiary or possibly somewhat earlier.

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[10] [An interesting piece of work on this subject is H. P. Crampton's "The Zoological Facts of Distribution in Relation to the Problem of Subsidence in Polynesia," not yet published, and his "Studies on Variation, Distribution and Evolution of the Genus Partula; the Species Inhabiting Tahiti," Carnegie Inst. of Washington, Publ. 228, 1917.—Ed.]

We may then conclude that the bulk of the vegetation in Hawaii is made up of residual types, *i.e.*, remnants of a flora common to the ancient much larger Hawaii, and the continental masses to the South. These ancient types have become more or less changed since the isolation of the Archipelago, and their number has been augmented by a relatively small number of forms introduced from America subsequent to the isolation of the Islands.

SUMMARY

The Hawaiian islands present extremely varied environmental conditions: mountains nearly 14,000 feet high give temperatures ranging from tropical heat to almost perpetual snow; the yearly precipitation ranges from less than 20 to over 500 inches; the soil varies from fresh lava to old well-disintegrated lava and alluvial valleys; the topography is rugged.

Practically all of the arable land of the lower elevations is cultivated.

Elimination of the undergrowth by man or grazing animals destroys the forest through exposing the trees and permitting the intrusion of Hilo grass.

The islands contain large numbers of endemic plants.

Only 6 strictly American genera occur in the Hawaiian Islands as compared with over 50 extra-American genera common to the islands and to regions of the Southern Pacific and Indo-Malaysia.

The large number of delicate forms whose seeds and spores could not survive transportation four or five thousand miles indicate a former land connection with the Southern Pacific islands. The ancient types forming the bulk of the vegetation have become more or less changed since the isolation of the Hawaiian Archipelago.

CHARTING QUADRATS WITH A PANTOGRAPH

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The quadrat method of recording changes in the composition of vegetation has been used by the Forest Service in connection with its various grazing investigations for a number of years. The accurate history thus compiled of the changes in plant formations, especially under different conditions of grazing, is invaluable in developing principles of range management. On the Santa Rita Range Reserve, in southern Arizona, eighty chart quadrats are mapped each year and as many more will be established in the near future. It is obvious to those familiar with quadrat charting that the mapping of this number of quadrats involves a great deal of work.

The method of charting heretofore followed is the common one in which straps are used to divide the quadrat into square decimeters, and the vegeta-

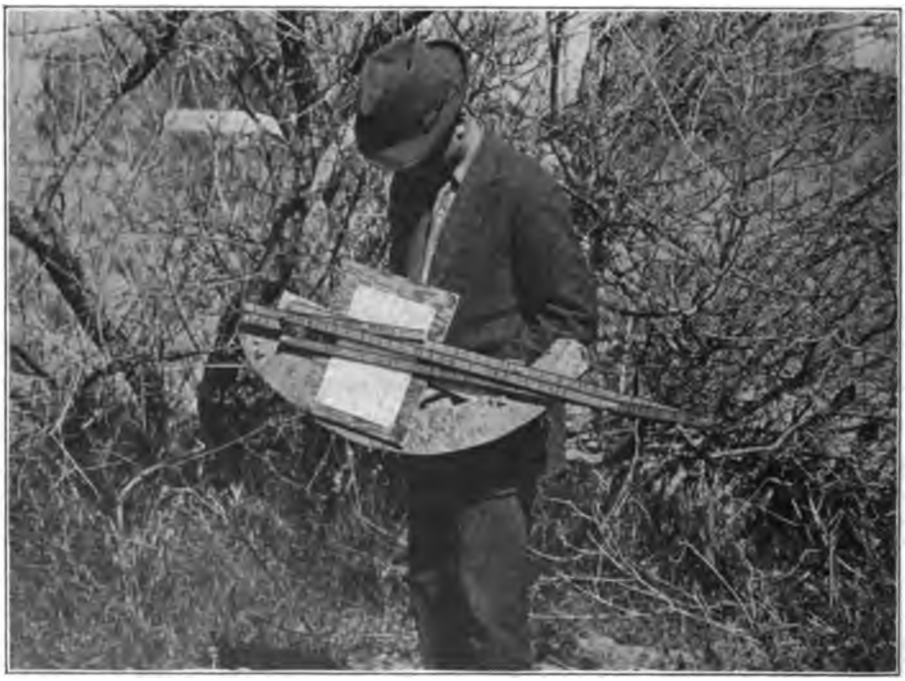

FIG. 1. Pantograph used for charting quadrats, folded for carrying.

tion within each decimeter is mapped on a reduced scale by ocular estimate, supplemented by actual measurement. The recognized disadvantages of this method led the writer to experiment with the pantograph as a practical means of avoiding them. Now, the pantograph is commonly considered as adapted for use only when operated upon a drafting table. For mapping vegetation in the field it would seem quite unusable. Nevertheless the experiments showed surprisingly good results. In fact, when mounted upon a suitable frame the pantograph registers the outline of vegetation as accurately as though the work were done on a drafting table. This is not to say that the result of this method of charting is a perfect reproduction of the outlines of vegetation; it is simply an accurate tracing of the outlines which were followed by the operator. The production of accurate charts is largely a matter of acquiring system and skill in guiding a needle around the outlines of plants.

As a result of the experiments with the pantograph the instrument was used in charting most of the established quadrats at the Santa Rita Range Reserve in the fall of 1919. The instrument (fig. 1) used is of wood with arms 40 inches long and set to reduce to 1/3.75 which, when applied to a meter quadrat produces a square approximately 10.5 inches on a side. A table 21 inches square, made of three-ply veneer and with demountable legs 10 inches high, was used to support the pantograph, which was mounted on a pivot at one corner. A metal leg 1 inch high with a ball roller, and attached to one arm, supported the instrument and, when the instrument was being used, swung back and forth across the table. The only other modification of the instrument was the substitution of a steel needle 10 inches long for the short needle used in tracing the outline of the figure to be reproduced. The needle not only supported one arm of the pantograph when not in motion but also enabled the outlines of the vegetation to be traced while the instrument remained high enough to be out of contact with the stems of the plants. The form for registering the charts was placed on the table after the instrument was set in position along one edge of the quadrat, and adjusted so as to record properly and then fastened with thumb-tacks.

It requires the services of two persons to chart successfully; one, who should be skilled in charting and familiar with the flora, to trace the outline of the vegetation and call out the proper symbols; the other to record the symbol for each species and to lift the recording pencil from one outline to the next. The equipment can be carried handily by the operators either on foot or on horse. An average day's work as conducted at the Reserve was the charting and describing of fifteen quadrats, although as many as twenty were completed in one day. An average day's work for one man using the hand method is four or five quadrats.

The advantages of charting meter quadrats with the pantograph as compared with the use of straps are:

1. The results are fully as accurate; the pantograph will record as accurately as the skill of the operator in following the outline of plants will permit.

2. The pantograph can be used with entire disregard of the presence of rocks or impenetrable soil—factors very important in using straps.

3. The rank growth of vegetation is even less of an obstacle to accuracy with the pantograph than it is with the strap method, because the foliage can readily be held with one hand while the outline of the plant is traced with the other. Where straps are used the rank foliage is very apt to prevent the straps from lying accurately in position.

4. The work can be done more rapidly with the pantograph and with much less tedium. (Two persons, only *one* of whom need be skilled, can chart fully three times as many quadrats with the pantograph as one skilled person can chart with straps.)

5. The pantograph is especially efficient in locating individual seedlings or one-stemmed plants and in tracing the outline of crowns of low bushes.

The principal disadvantage so far encountered in the use of the pantograph is the fact that the instrument is more cumbersome than the equipment used with the strap method. This is believed to be offset by the shorter time required to set up the pantograph. Moreover, the perfected instrument should be very easily carried and manipulated. The pantograph can be used on any degree of slope where quadrats are apt to be located; is equally useful whether the vegetation is scattered or dense; or whether it consists of perennials or annuals, and the data can be as readily compiled as the data obtained with the hand method, for in either case standard forms should be used in charting.

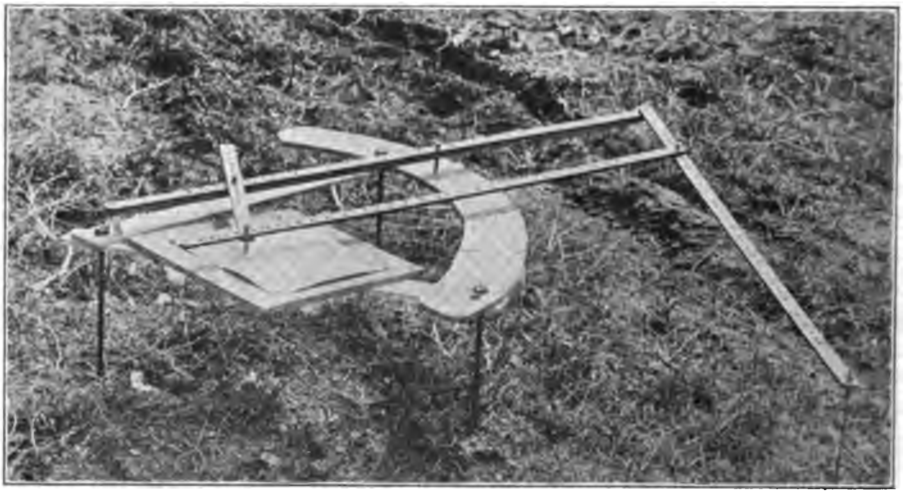

FIG. 2. Pantograph used for charting quadrats, set up ready for use.

Before general use is made of the pantograph in charting, the scale of reduction should be standardized. In future work at the Santa Rita Reserve it is planned to use the scale of 1 to 5. This is a convenient scale for mapping meter quadrats since the reduced base is 2 decimeters square.

The principal improvement which is needed in the instrument is a stand which can be quickly and easily set up; which will be rigid when in use; capable of being folded into compact form and strong enough for field use. The accompanying illustrations (figs. 1 and 2) are of a rough model of a stand designed to embody these qualities. The finished stand will consist of a frame shaped like a sector of a circle, mounted on three legs and supporting a map-holder. The frame will have two arms reaching out from a pivot, on which the pantograph will be mounted, to a curved track where will run the ball-bearing peg used to support the weight of the pantograph and enabling it to be moved smoothly back and forth through an ark of about 90 degrees. The arms will be 25 inches long and two inches wide. The track will be 42 inches long, measured on the outer edge, and 3 inches wide. The map-holder will be 12 inches long and 10 inches wide. The material for these parts will be quarter-inch hardwood reinforced with brass strips. The legs will be of metal; will be bolted onto the frame and made to fold up. The map-holder will be attached to one arm of the frame by means of a bolt which will slide along a slot set diagonally across the under surface of the holder and along a slot of similar length on the arm. This arrangement will allow the holder to be adjusted readily into any position so that the recording pencil will register properly with reference to the position of the quadrat. The record sheets will be held in place by spring clamps. The pantograph will be attached by means of a spring socket on the end of the pivot arm which will fit onto a peg with a ball head. This peg will be an extension of a bolt which will also hold the arms together. By removing this bolt and bringing the arms together toward the track, the stand may be folded quickly and in this position can be carried handily.

It is not presumed that the instrument just described will need no refinements. Continued use of the instrument will doubtless suggest several improvements. The experience already had, however, of charting quadrats with the pantograph has convinced the writer that the method is thoroughly sound and should reduce the burden commonly associated with this phase of ecological work.[1]

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[1] It is not known what it will cost to manufacture the charting pantograph but it is believed that the price should not exceed twenty dollars.

PLANTS AND ANIMALS OF MOUNT MARCY, NEW YORK, PART III

CHARLES C. ADAMS, GEORGE P. BURNS, T. L. HANKINSON, BARRINGTON MOORE, AND NORMAN TAYLOR

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V. TREE DISTRIBUTION AND EXPOSURE

Above timber line[36] in the shelter of certain rocks are found compact groups of stunted balsam firs, while beside others is alpine vegetation. What is it that permits dwarf trees to become established in certain places and not in others?

In the Selkirk mountains of British Columbia Shaw[37] found that timber was lacking in the depressions above approximately 6,000 feet, but extended above this elevation on knolls and ridges. He explains this as due to late melting snows and black fungus which is left on the trees after the snow. It has also been shown by Cowles that in a number of places in North America snow beds and timber line are causally related. Bouget[38] working in the Pyrenees found mesophytic herbaceous communities of mixed lowland and alpine plants where the snow lies late, and trees on the ridges at the same elevations. Thus timber line in the Pyrenees, as in the Selkirks, runs higher on the ridges than in the depressions. Examples of lowland communities where the snow lies late on Mt. Marcy are described above in Part II under the "Dwarf Birch Meadow" and "Meadow on Southeastern Side of the Mountain at 5,100 feet" (ECOLOGY, Vol. 1, No. 3 pp. 220–226). Aside from these two examples, conditions on Mt. Marcy appear to be the reverse of those found in the Selkirks and in the Pyrenees, for on Marcy the trees push upward in the ravines, not on the knolls and ridges. But on Mt. Marcy there are no extensive slopes above timber line to collect snow, whereas in the Selkirks and Pyrenees masses of snow probably come down from above into the ravines, preventing the development of trees by avalanches and by occupying the ground late in the growing season. Hence on Mt. Marcy the trees extend to higher elevations in the ravines than elsewhere.

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[36] See definition of timber line as used in this study, ECOLOGY, Vol. I, No. 2, p. 72.

[37] Shaw, C. H. "Causes of Timber Line on Mountains," Plant World, Vol. 12, No. 8, pp. 169–181, 1909. "Vegetation and Altitude," Am. Naturalist, Vol. 43, pp. 420–431, 1909.

[38] Bougert, J. "De l'influence des neiges sur la repartition des differents végétaux a même altitude dans les zones elevees des Pyrenees," Rev. Gen. Bot. 30: 305–320, 1918, Bot. Gaz. 69: 533, 1920.

It has been supposed that the stunting of trees in arctic regions and on Mountains is due to the winds withdrawing moisture from the needles at times when the frozen ground prevents the roots from replacing this moisture. But recent work on the transpiration of conifers in winter has shown that "the winter transpiration losses from conifers are scarcely greater than those from the defoliated stems of broad-leaf trees."[39] It therefore appears that the winter winds may not be the only cause affecting tree distribution on mountains.

In considering the influence of wind on tree distribution in the alpine zone it is necessary first of all to know something of the winds to which the open places and the groups of stunted trees are exposed. Would not the direction of the shelter with relation to the wind play some part in permitting or preventing tree growth? Information on this question might throw light on the relation of wind to timber line. On Mount Marcy the prevailing winds are from the northwest and the west.

A map (fig. 21) of a portion of the summit above timber line was made by means of a rough plane table, compass and tape. The last was used only between stations, the size of the tree groups, open areas (alpine vegetation), and rock masses, being obtained by pacing. The direction of the winds to which each area is exposed was noted and recorded on the map by arrows. The survey was run along the 5,000 foot contour, starting at a point on the south trail where a metal plug marked "O 107" was found set in a rock dome. The point is marked ".07" instead of "O 107" in the lower part of the map (see fig. 21) where the contour makes a bend at right angles from a north-south to an easterly direction. (Figure 2 in Part I (ECOLOGY, Vol. 1, No. 2, p. 74) was taken at approximately the point ".07," looking north. The main map shows south, west, and northwest exposures; the small insert map gives a typical case of north, northeast and east exposures. In addition to showing exposure to wind the map gives a general idea of the relative proportions of dwarf trees, alpine vegetation (marked "open grasslands" on the map), and bare rock in the lower part of the alpine zone. The proportion of dwarf trees is less above 5,000 feet. Collections of animals, listed further on, were made along the survey line.

In general, the degree of shelter required against south, southwest, and west winds is less than that required against northwest winds. The insert may indicates that easterly winds are also of lesser importance. It will be noticed that on the map a large proportion of the open areas are exposed to the northwest winds, while not a single tree group shows exposure to winds from this direction. On the north side of the mountain, however, not included in the map, is a large body of stunted balsam firs extending well above timber line and exposed on the northwest. But these trees occur in deep, moist ravines almost certainly filled with snow in winter.

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[39] Weaver, J., and Mogensen, A. "Relative Transpiration of Coniferous and Broad-leaved Trees in Autumn and Winter," Bot. Gaz. 68: 393–424, 1919.

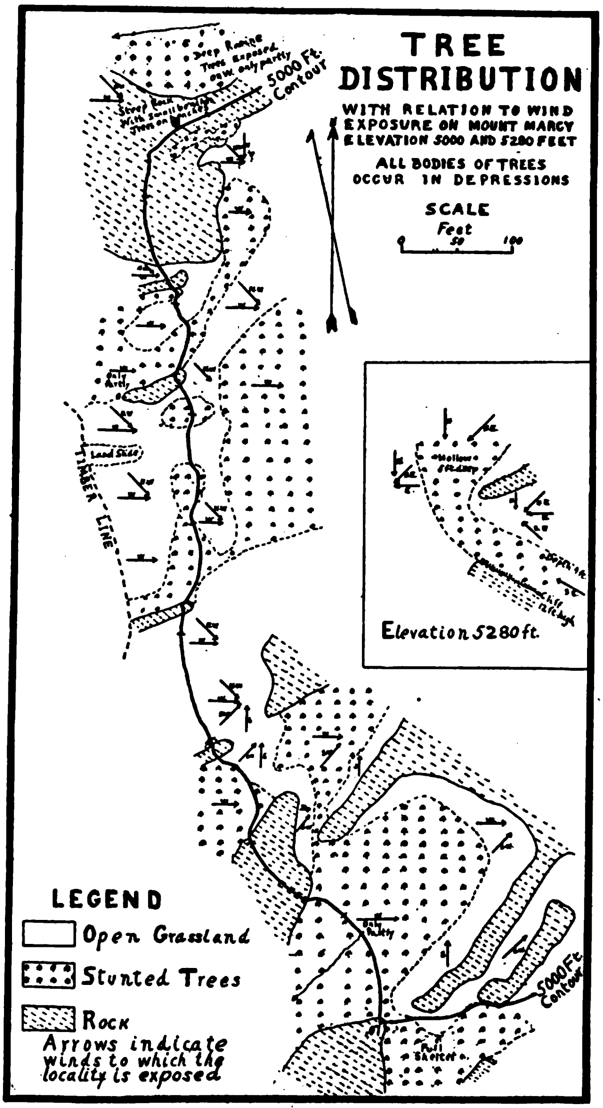
TREE DISTRIBUTION
WITH RELATION TO WIND EXPOSURE ON MOUNT MARCY ELEVATION 5000 AND 5280 FEET
ALL BODIES OF TREES OCCUR IN DEPRESSIONS
SCALE
Feet
0 50 100
Deep Ravine Trees exposed on W. only partly
5000 Ft. Contour
Steep Rock With small bodies Trees on ledges
Only Partly
Land Slide
TIMBER LINE
Hollow Swamp
Cliff 12 ft. high
Elevation 5280 ft.
Shelter
5000 Ft. Contour
LEGEND
Open Grassland
Stunted Trees
Rock
Arrows indicate winds to which the locality is exposed

FIG. 21. Map showing distribution of vegetation with relation to wind exposure. The "open grassland" should be called alpine vegetation, and the number .07 near the bottom should be O107. Areas of stunted trees without arrows may have the tops exposed, but the trees themselves are fully sheltered.

The most striking fact noted during the mapping was that the trees are confined to the depressions.

The only exception, which tends to emphasize rather than to refute the rule, is an occasional flattened black spruce, *Picea mariana,* and balsam fir, *Abies balsamea,* hugging the ground in an opening. These prostrate trees, though not uncommon are by no means abundant, and illustrate in a striking manner the extreme precariousness of tree life outside of the depressions. As a general rule the height of the trees corresponds with the depth of the depression. The trees form a dense and uniform crown canopy at a certain level. Above this uniform canopy the leaders protrude. Only a few are uninjured, many of them are dead, and others are dead on one side. These leaders bear witness to the desperate struggle between the trees and the elements. The trees unceasingly endeavor to extend upward, the elements as steadily kill them back to a certain level. The injury to the partly killed leaders is on the northwest side in the majority of cases. Leaders fully exposed to the north, northeast and northwest winds invariably showed injury on the northwest. Trees on a southerly aspect (S. 22° W. to be exact) showed some injury from the west, a little from the south, but most from the northwest which must be due to the high winter winds sweeping around the mountain. This shows the power of the northwest wind.

Just how the wind acts upon the growth of the trees could not be definitely ascertained. It may be that the canopy level represents a line below which the force of the wind is so lessened by the configuration of the ground that the trees are not injured. Or it may be, and this seems more probable, that the canopy level corresponds with the depth of the snow in winter; the leaders extending above the snow being injured and eventually killed. Variation from year to year in the depth of the snow above a certain level represented by the tree canopy would account for some of the leaders being still uninjured. The nature of the injury does not seem to indicate a high degree of mechanical or "sand blast" action which would come from particles of ice driven with great force. There is none of the etching out of the wood such as is found on the high mountains of the west. Undoubtedly much of the injury is due to mechanical action of a less intense form, but some of it may also be due to drying out by the sun and wind above the snow.

From the area of stunted trees shown at the base of the map (fig. 21) and along its margin were taken the spider *Pardosa musicola* Em., the lady bird beetle *Coccinella transversoguttata* Fab., the leaf hopper or jassid *Oncopsis fitchi* VanD., the alpine wingless grasshopper *Podisma glacialis glacialis Scudd.*, and the grasshopper *Melanoplus atlanis* Riley. Along the survey line, about 400 feet to the northwest in an open grassy area was taken the spider *Pardosa musicola* Em., the grasshopper *Camnula pellucida* Scudd., and *Melanoplus atlanis* Riley, the fly *Bibio longipes* Leow., and the ant *Formica sanguinea* Latr., subsp. *aserva* Forel. At about 425 feet northwest of the starting point was a deep crevice in the rock, facing west and with dripping wet sides. Near this crevice was an area of sedges, *Vaccinium* and *Cladonia,* with prostrate black spruce, and about a foot of sand and humus soil. Here was taken the spider *Pardosa musicola* Em., the grasshoppers *Melanoplus atlanis* Riley, and *Circotettix verruculatus* Kby., the bug *Lygrocoris diffusis* Uhl., the fly *Bibio xanthopus* Wied., and the ant *Camponotus herculeanus* L., subsp. *ligniperda* Latr., var. *noveboracensis* Fitch. At about 900 feet along the survey line a large ravine is encountered. The general character of this area is shown in figure 3, Part I, p. 75. The collections from the vicinity included the spider *Pardosa distincta* Black., *Lycosa albohastata* Em., the grasshopper *Melanoplus atlanis* Riley, a bug *Nabis subcoleopterous* Kby., a caterpillar, an ichmeumon *Amblyteles funestus* (Cress.), a muscid fly *Pollenia rudis* Fab. (infested with a fungus), the fly *Bibio xanthopus* Wied., and the ant *Formica sanguinea* Latr., subsp. *aserva* Forel. The only specimens of the large grasshopper *Circotettix* were taken along this line. They show a preference for bare rock, as in the specimens taken at the beginning of this survey line, when their hovering flight was observed. The fly *Pollenia* is reported as a parasite on earthworms.

VI. Influence of Altitude on Tree Growth

The Mount Marcy region is particularly favorable for studying the influence of altitude on tree growth because one tree species, balsam fir, is found from the lower elevations almost to the summit. Since, however, this study is concerned primarily with timber line and the habitats just above and below it, the records of tree growth were taken at the following points: (1) The lower limit of the pure fir forest, 4,250 feet; (2) at timber line, 4,890 feet, on the extreme upper edge of the continuous forest just below the alpine vegetation; and (3) in the tree groups above timber line at 4,980 feet, with a few at 5,000 and at 5,200 feet.

The growth figures were obtained by means of a Swedish increment borer twelve inches in length. With such small trees it was possible to take cores clear through from one side of the tree to the other. This enabled correction to be made for trees in which the rings were wider on one side of the trunk than the other. The boring did not always strike the centre, but this made no difference since care was taken not to include measurements which were off the radius. It was not practicable to secure figures on total age, nor are such figures essential in determining the rate of growth. Most measurements were taken at a height of twenty centimeters above the ground, the lowest point at which the increment borer can readily be manipulated. In some cases the measurements were taken at thirty centimeters, in exceptional cases higher. Since the total age was not secured the height of the core was of importance chiefly in avoiding the butt swelling. Only dominant trees were taken. The width, in millimeters, of each ten years was measured in accordance with the usual forestry practice.

The accompanying curves (fig. 22) show graphically the rate of growth in diameter inside bark of balsam fir at the different elevations. These curves were constructed by the usual forestry method, plotting the points for each decade, and averaging these points. A remarkable feature was the regularity with which the curves passed through the average points, it being unnecessary, except in minor cases, to "smooth off" the curves by ignoring points out of line.

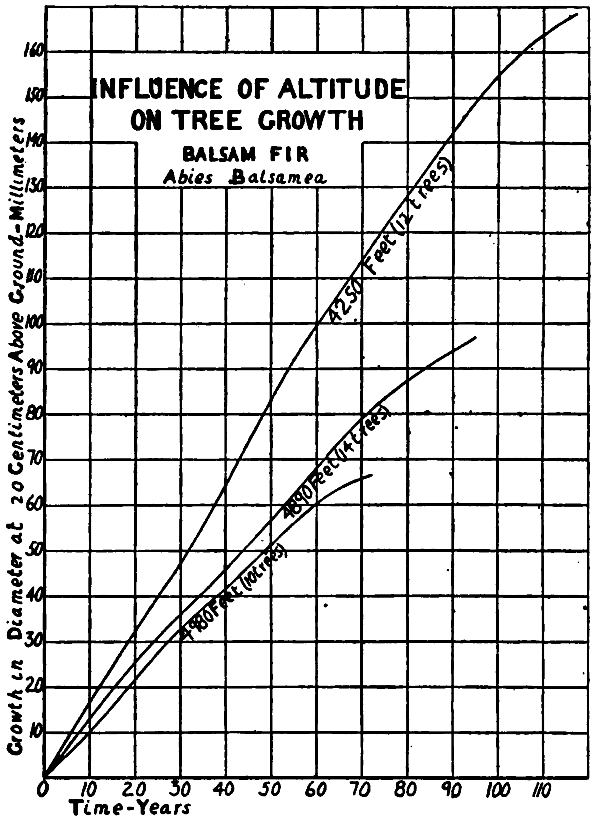

FIG. 22. Rate of growth in diameter inside bark of balsam fir at different altitudes on Mt. Marcy.

Table 5 gives the diameter inside bark at each ten year period, taken from the curves, and also the average annual growth for each decade. It will be noticed that the rate is not uniform throughout the life of the tree. Table 6 gives the age at each centimeter of diameter inside bark, taken from the curves.

TABLE 5. *Growth of balsam fir in diameter inside bark at different altitudes*

Time, Years	Diameter inside bark at each 10 year period, millimeters			Average annual growth in each 10 year period, millimeters		
	At 4,250 ft. elevation	At 4,890 ft. elevation	At 4,980 ft. elevation	At 4,250 ft. elevation	At 4,890 ft. elevation	At 4,980 ft. elevation
10.....	16.8	13	10	1.7	1.3	1.0
20.....	32	25.3	21.5	1.5	1.2	1.2
30.....	47	36	32.7	1.5	1.1	1.1
40.....	64	45.7	41.5	1.7	1.0	.9
50.....	83	56.6	51.2	1.9	1.1	.9
60.....	99.5	68	60.3	1.6	1.1	.9
70.....	114	79	65.7	1.5	1.1	.6
80.....	128	87.4		1.4	.8	
90.....	142	94		1.4	.7	
100.....	154.8			1.3		
110.....	164			.9		

TABLE 6. *Age of balsam fir at each centimeter of diamcter inside bark at different altitudes*

Centimeter inside bark	Age, years		
	At 4,250 ft. elevation	At 4,890 ft. elevation	At 4,890 ft. elevation
1...............	6	8	10
2...............	12	16	19
3...............	19	24	28
4...............	25	34	38
5...............	32	44	49
6...............	38	53	60
7...............	43	62	
8...............	48	71	
9...............	54	84	
10...............	60		
11...............	67		
12...............	74		
13...............	81		
14...............	89		
15...............	96		
16...............	105		

The decrease in rate of growth is not in exact ratio with increasing altitude. The average annual growth for the first 60 years at each of the three elevations represented in the curves is as follows:

At 4,250 feet, average annual growth of first 60 years	1.65 mm.
At 4,890 feet, average annual growth of first 60 years	1.13 mm.
At 4,980 feet, average annual growth of first 60 years	1.01 mm.

Plotting these values we find that the decrease per unit of elevation is greater between 4,890 and 4,980 feet than between 4,250 and 4,890. It appears therefore that rate of growth diminishes with altitude, and that at a certain point (the beginning of alpine vegetation in this case) the diminution per unit of elevation becomes more rapid.

The curves show that the influence of altitude is exerted not only upon the rate of growth, but upon the longevity of the trees. It will be noticed that at 4,980 feet the growth rate drops off at 60 years. At timber line the rate continues for 70 years (68 to be exact), while at 4,250 the final drop in rate does not occur before 95 years, although there is a decrease after 50 years. Thus, at the higher elevations the trees not only grow more slowly but are shorter lived; on the other hand, decay seems to be more prevalent below timber line.

VII. Growth Forms of Plants

In considering the response of the vegetation above timber-line, it seems best to omit from our calculations several species credited to the region and either so rare or actually wanting now that they are scarcely of significance. The omitted species, for the purposes of sorting into the Raunkiær growth-form categories, are *Juniperus communis, Carex vitilis, Carex concolor, Epilobium angustifolium, Kalmia glauca, Melampyrum latifolium, Rhinanthus crista-galli* and some others. This leaves 60 species which certainly make up 99 percent. of the vegetation above timber line.

In sorting these into the Raunkiær[40] growth-form categories all woody plants, because of their dwarf habit, have been classed as nanophanerophytes, except those that would naturally go in with the chamaephytes. It may be objected that the fir, black spruce, paper birch, and *Sorbus scopulina* are trees and should consequently go in categories calling for greater stature than nanophanerophytes. The best answer to this is that on the open summit outside of sheltered depressions they are never over 3 feet, and usually flattened against the ground. The flora above timber line, so far as the growth forms are concerned appears to be separable as follows:

Nanophanerophytes	13	or	21.66	percent.
Chamaephytes	9	or	15	percent.
Hemicryptophytes	29	or	48.33	percent.
Geophytes	9	or	15	percent.

As these figures and percentages are of value only in comparison with other regions, and only thus do they indicate response of plants to varying environments, the following table is submitted.

It will be seen from this that the vegetation on the top of Marcy is much like that on the Labrador Coast or in Spitzbergen, notably in the failure of trees of any height to develop, and in the high percentage of perennial herbs. It would be an interesting study to determine, as one of the authors has done for Long Island, N. Y., how these percentages would be effected by considering individuals rather than species. All that could be considered with the time at our disposal were the species, but a more extended study would no doubt result in changes if only the species which make up the bulk of the flora of the summit, were the ones considered.

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[40] Fuller, G. D., and Bakke, A. L. "Raunkiær's Life-forms, Leaf-size Classes and Statistical Methods." Plant World, Vol. 21, pp. 25–37, 1918.

Smith, W. G. "Raunkiær's Life-forms and Statistical Methods." Jour. Ecol., Vol. 1, pp. 16–26, 1913.

TABLE 7. *Biological spectrum of the flora above timber line on Mt. Marcy, as illustrated by Raunkiær's growth-forms, in percentages. (The normal spectrum, and other regions included for comparison.)*

Type of growth form	MG	MS	MC	N	CH	H	G	HH	T
Normal spectrum	6		17	20	9	27	3	1	13
Flora of vicinity of N. Y.	.52	4.03	7.18	3.51	5.29	33.29	20.23	11.74	13
Flora of vicinity of N. Y. Northern element of it only		1.31	3.94	8.55	8.55	26.31	24.32	23	3.94
400 commonest species on L. I., N. Y.	1.50	3.00	8.50	4.25	7.25	30.00	21.00	6.75	14.25
Baffin's Land				1.00	30.00	51.00	13.00	3.00	2.00
Iceland				2.00	13.00	54.00	10.00	10.00	11.00
Spitzbergen				1.00	22	60.00	13.00	2.00	2.00
Labrador Coast		2.00	1.00	8.00	17.00	52.00	9.00	5.00	6.00
Above timber line on Mt. Marcy, N. Y.				21.66	15.00	48.33	15.00		

The figures given, however, are in line with those from the arctic-alpine regions where the chamaephytes and hemicryptophytes are relatively high in number, In the last five localities of the above table, including the summit of Mt. Marcy, there are practically no trees.

So far as species are concerned, it is not without significance that by leaving out of the count those plants that have come up through the fir forest to the summit, we find the remaining element of the vegetation, which may be considered certainly as alpine or sub-alpine to consist of:

N—6, CH—9, H—14, G—-.

While the element that has come up from below and seems an obvious encroachment into the alpine zone consists of:

N—8, CH—-, H—15, G—9.

No attempt has been made to give growth-form percentages from the station *a* at the 4,250 ft. elevation. If *species* were considered here the fir would only figure as one, while if individuals were reckoned it would show 85 percent. of the forest as fir. In nearly exclusive forests of the sort, the Raunkiær growth-form percentages may obscure, rather than elucidate, the truth about vegetative response to climate, while in the alpine zone they give interesting comparisons with the flora of other parts of the world.

VIII. SUMMARY AND CONCLUSION

The methods of study and viewpoints of zoologists, botanists, and foresters have been brought together for a brief cooperative study of the factors causing the sharp differentiation of habitats at timber line on mountains. Timber line was taken as the end of the continuous forest, except in depressions, and beginning of alpine vegetation; this occurs on Mt. Marcy at approximately 4,900 feet elevation.

Mount Marcy is 5,344 feet high, possessing above timber line a relatively small area of rather uniform relief exposed on all sides. A well-defined cirque was found on the north slope at 5,250 feet.

Geologically the region is one of the oldest mountain areas of the world, mountains being formed and worn down repeatedly. There has been much faulting. Scouring and filling by glacial ice and waters was followed by depression and reelevation.

The rock forming Mount Marcy is a resistant, coarsely crystalline, greenish colored anorthosite resulting from the thrusting of molten masses into overlying sedimentaries including limestone. The rock contains approximately 10 percent. of lime, which, however, is not readily available to plants.

The climatic winter of the summit, if snow be the criterion, commences in the latter part of September or early October and ends in June, giving barely two months of summer. Previously no weather records have been kept on the mountain. Records for five stations 37 miles air line from the summit or nearer, and over 1,000 feet in elevation, give a mean annual temperature of 42.13° F. south of the mountain and 39.54° north of it, with mean maxima of 92° and 95°, and minima of —36° and —28° respectively. The growing season for the region of which Mount Marcy is roughly the centre averages 92 days, as compared with 120 for the Catskills and 200 on Long Island. Precipitation is distributed rather uniformly over the year, and is on the whole high and sporadic.

To determine as far as possible the relative differences in the climatic factors influencing the various habitats, brief instrumental records were secured of evaporation, solar radiation, air temperature and soil temperature at the critical points in the vegetative covering. These points were (*a*) the lower limit of the fir forest at 4,250 feet, which from here up forms a uniform vegetative unit extending to timber line; (*b*) the bog at the east end of Lake Tear (headwater of the Hudson River) at 4,320 feet; (*c1*) the dwarf fir forest just below timber line at 4,890 feet, in the tree crowns; (*c2*) the same as (*c1*), but on the ground under the dense forest; and (*d*) the alpine zone just above timber line at 4,920 feet.

The rate of evaporation tends to increase with elevation, except that the rate in the bog was higher than that just below timber line. The rate under the cover of the dwarf fir forest was lowest of all owing to shelter from sun and wind.

Solar radiation shows a similar relation to altitude. Taking that above timber line as 100 percent, the stations were: (*d*) 100 percent, (*b*) Lake Tear bog, 99 percent, (*c1*) crown of dwarf forest, 89 percent, (*a*) lower limit of fir forest, 51 percent, and (*c2*) under dwarf forest, 4 percent.

The average daily range of air temperature (difference between maximum and minimum) increased with altitude, except that the range just below timber line was a trifle greater than that just above.

Summations of temperature above 40° F. showed that the heat available for growth diminishes with altitude except for the bog. A sharp drop in effective temperature between the station just below and that just above timber line corresponds with the abrupt contact between the two life zones, and suggests that the amount of effective temperature may be a leading factor in causing the sharp line of demarkation at timber line.

Soil temperature at 1½ inches was highest in the bog, and a trifle higher in the alpine zone than at the lower limit of the fir forest. But at a depth of 12 inches the soil temperature appears to decrease with increasing altitude.

Analyses of a limited number of soil samples showed the dry matter to contain from 12.24 to 21.93 percent of organic and volatile substance and from 1.75 to 2.31 percent of nitrogen (save for an exceptional sample which contained only .79 percent of nitrogen). All showed a high lime absorption coefficient, indicating high acidity in spite of the high lime content (10 percent) of the underlying rock.[41]

The fir forest is of nearly uniform composition from 4,250 feet to timber line, being practically pure *Abies balsamea* with only a small scattering of paper birch, *Betula papyrifera.* The height and diameter of the firs diminishes with altitude from approximately 45 feet high by 8 inches in diameter to 10 feet by 3 inches. Fir reproduction is abundant wherever the canopy is not too dense. The dominant herb of the moss covered forest floor in the lower part of this forest is bunch berry, *Cornus canadensis,* and in the upper part is *Oxalis Acetosella.* Most of the plants of the understory, even up to timber line, are on the whole plants of lower and moderate elevations.

The chief bird habitat is below the area included in this study. In the fir forest juncoes, golden-crowned kinglets and myrtle warblers were the most abundant of the few species seen, though some twenty other kinds of birds have been previously recorded from here. Little evidence of mammal life was seen in the fir forest, aside from deer and red backed and white footed mice, though other mammals have been reported. No amphibians, except a frog at 4,300 feet and toad at 4,500 feet were found, and probably the short summer prevents their living here. In the upper part of the fir forest, where the trees are dwarfed and extend in locally protected depressions above timber line, no mammals were found except the red backed mouse, which seems to be established here, and signs of the varying hare. Several birds were noted.

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[41] Dr. Edgar T. Wherry of the U. S. Bureau of Chemistry has kindly examined a specimen of similar anorthorite from Mt. McIntyre since Part I of this paper was published. He finds that the calcium is combined in the form of silicates which are comparatively insoluble and form the feldspar known as labradorite. There is no evidence that lime is present to any extent as carbonate.

The vegetation of the Lake Tear bog consists of bog plants, *Carex oligosperma* dominant near the lake and *Calamagrostis neglecta* dominant elsewhere, with a few alpines, notably the crowberry *Empetrum nigrum,* and scattered young fir trees at one end. The alpine plants occur only in this bog and above timber line, being absent from the intervening belt of fir forest. The invertebrates collected in the bog were mainly species living in the open rather than in the forest. Of special interest is the grasshopper *Podisma glacialis glacialis,* which like the crowberry, was also found in the alpine zone.

In two meadows well above timber line are found a number of lowland plants, one of them, *Calamagrostis canadensis,* being dominant, and some of them not hitherto recorded from above timber line on Mount Marcy. In these meadows were also collected animals from lower altitudes, showing the encroachment of lowland animals as well as plants into the alpine zone.

Of 73 species reported by Peck from the alpine zone, 21 may have disappeared or at least were not seen by us. Of 7 species not reported by Peck and which apparently have come in since 1879 or later, it is significant that none are true alpines and 4 are certainly encroachments from lower down the mountain. Only 23 species are true alpines, and at least 30 have apparently come up through the timber line from the forest below, dwarfed in stature and changed in color, but still flowering and fruiting. Not one case of invasion from the alpine zone into the fir forest below was found. The evidence of the plants shows that the alpine forms are not spreading downward and may even be vanishing while the lowland forms are pushing upward, indicating that the northward migration which followed the retreat of the ice sheet is still going on.

In studying the relation of wind exposure to stunted trees above timber line a map was made along the 5,000 foot contour showing clumps of stunted trees and open areas, with arrows indicating the direction of the winds to which each locality is exposed. The map indicates that trees require more shelter against northwest winds than against winds from any other direction, and are confined to the depressions. As a rule the height of the trees corresponds with the depth of the depression, and the trees form a very dense canopy at a certain level which probably corresponds with the depth of the snow in winter. The trees continually send up leaders above this level, which are gradually but surely killed back. The injury to leaders above a certain level is generally on the northwest, and does not indicate a high degree of mechanical or "sand blast" action. Collections of animals were made along the survey line of the map from the groups of stunted trees, from the open, and from the bare rock.

The rate of growth in diameter of balsam fir was measured at 4,250 feet, 4,890 feet, and 4,980 feet. Growth decreases with altitude, but not uniformly, the decrease being more marked at timber line. Longevity of the trees also diminishes with altitude.

An analysis of the vegetation above timber line in accordance with Raunkiær's growth-forms permits comparison with the "biological spectrum" of other regions and shows that the vegetation of the top of Mount Marcy is much like that on the Labrador Coast or in Spitzbergen. The "spectrum" of the alpine and sub-alpine element of Mount Marcy shows significant differences from that of the plants which have invaded the summit from below.

One of the most interesting conclusions of this study is that the plants and animals of the alpine region are evidently not spreading downward but that there is a distinct upward extension of the lowland forms. The peak of Marcy forms a small open area (like Lake Tear) in an area of fir forest, the climax forest. This forest tends to take complete possession of all open spaces and it naturally encroaches upon alpine or bog areas. In this we see the intimate relation between local and geographical influences.

Observations and brief instrumental records of climate on Mt. Marcy seem to suggest that the most important factors in causing the timber line on mountains are effective temperatures, wind, and the depth of snow. It is not unlikely that the contrast between the open and the forest vegetation is more important to animals than the change in the physical conditions, although the two can not be wholly separated.

In conclusion we wish to urge the need of both photographic surveys and the detailed mapping of the timber lines on our mountains; and attention should also be given to photographs showing the stages of melting snow.

In working up the collections assistance was generously given by the following who determined specimens submitted to them:

Charles P. Alexander, Illinois State Natural History Survey. Tipulid.
Charles T. Brues, Bussey Institution, Harvard University. Parasitic Hymenoptera.
Nathan Banks, Museum Comparative Zoology, Cambridge, Mass. Phalangids and Psocid.
R. V. Chamberlin, Museum of Comparative Zoology, Cambridge, Mass. Myriopod.
C. J. Drake, The N. Y. State College of Forestry, Syracuse, N. Y. Certain Hemiptera.
J. H. Emerton, Boston, Mass. Spiders.
Charles W. Johnson, Boston Society Natural History, Boston, Mass. Diptera and miscellaneous insects.
A. P. Morse, Wellesley College, Wellesley, Mass. Orthoptera.
Herbert Osborn, Ohio State Univ., Columbus, Ohio. Homoptera.
E. M. Walker, Univ. of Toronto, Can. Aeschnid.

W. M. Wheeler, Bussey Institution, Harvard University, Boston, Mass. Ants.

C. F. Batchelder, Cambridge, Mass. Mammals.

Kenneth K. Mackenzie. Sedges.

Ralph C. Benedict. Ferns.

R. S. Williams. Lichens and mosses.

The soil analyses were kindly made by C. H. Jones, Chemist of the Vermont Agricultural Experiment Station.

The Committee wishes to express its appreciation to the following persons and institutions for making this study possible:

To Dr. C. Stuart Gager, Director of the Brooklyn Botanic Garden at Brooklyn, N. Y.

To J. L. Hills, Director of the Vermont Agricultural Experiment Station, Burlington, Vt.

To Dr. Hugh P. Baker, at the time of this study Dean of The New York State College of Forestry at Syracuse, N. Y., through whom The Roosevelt Wild Life Forest Experiment Station cooperated.

Finally on behalf of the Ecological Society of America, the Chairman of the Committee wishes to take this opportunity of extending the Society's thanks and appreciation to all who have in any way helped in this investigation.

CORRIGENDA FOR PART II

On page 207, 7th line, after (p. 50) add "and there are as well many transient species" The sentence immediately following should read "Since less than 30 species of birds have been found above the hardwood zone (2,500 feet) and since the forests above this level are too dense to attract all but perhaps 15 species (Eaton,[18] p. 42)," . . . The first word in the 14th line should be Some instead of Other. In the 27th line ***hudsonitus*** should be ***hudsonicus***.

On page 209, 12th line, for "the chief source" read "a source."

On page 212, 13th line, "Prine" should be "Prime." The first word in the 13th line from the bottom should be "bellied" instead of "billed."

On page 214, 18th line, "*Ignobalis* Low" should be "*ignobalis* Loew." In the 23d line after the sentence ending "forest humus" insert the following: "*Conotyla* is recorded from under bark, among decaying leaves and other vegetation. Dr. R. V. Chamberlin, in a letter, writes: 'The only reference in literature to *Conotyla fischeri* is in Ann. N. Y. Acad. Sci., 1895, vol. 9, p. 71, the place of the original description. Cook gives the habitat as Central New York, stating that he had about 100 specimens from Onondaga, Wayne and Ontario counties. As to its habits he says, "at Marcellus several individuals were found under the loose bark of a fallen butternut tree (*Juglans cinerea*). All the other specimens were found among leaves and rotting vegetable matter in moist woods." Related species are known from caves (Indiana) and from mountains in the West from where I have described a number of species. I found them to prefer particularly deep, cool canyons in the bottoms of which they were often found in considerable numbers under accumulations of leaves. In general these and other forms of the same family are found in particularly moist situations, being more sensitive to conditions of dryness than most other diplopods. I may add that I have specimens of *Conotyla* taken under leaves in damp woods of Illinois, Minnesota, etc.'"

On page 215, 11th line, *Zoptrichia* should be *Zonotrichia.*

On page 216, footnote 30, pp. 1–267 should be 1–1267.

On page 221, under the title of fig. 18, the second sentence should read "This meadow contains plants and animals of lower elevations which are invading the alpine zone."

On page 223, 3d line, add: "The fir trees, about 10 feet high, growing at the mouth of the cirque are much distorted and their branches are broken by snow pressure." In the 7th line *subarinata* should be *subcarinata.* The title of fig. 20 should read ". . . containing lowland plants and animals . . ." In the second line below the figure *Cammula* should be *Camnula;* in the third *pholadice* should be *philodice*; and in the fourth *Componatus* should be *Componotus.*

On page 224 at the end of the 12th line insert "and injured dwarf firs."

On page 230, 8th line from the bottom, fig. 19 should be 20.

On page 231, 4th line, *supripennis* should be *cupripennis*; 20th line *terracola* should be *terricola;* 29th line *pellucia* should be *pellucida*; 31st line *pectrifrons* should be *pictifrons*; 33d line *ulteola* should be *lulteola*; next to last line *Mabis* should be *Nabis.*

On page 232, 3d line, Lats. should be Latr. In the 23d line *Melonaphus* should be *Melanoplus,* and *Femur* should be *femur.*

FACTORS CONTROLLING THE DISTRIBUTION OF FOREST TYPES, PART II

G. A. Pearson

Forest Examiner, Fort Valley Forest Experiment Station

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Determination of Factors Limiting the Distribution of Forest Types

The first phase of this study dealt with the measurement of soil and climatic factors in each forest type. The second phase seeks to apply the results in explaining the presence or absence on different sites of various tree species indigenous to the region, and then to determine the limiting factors in the distribution of each species and forest type. A more direct way would be to grow the trees under controlled conditions, but in view of the long life period of trees and their demands upon space, the physical difficulties in the way of such an undertaking render it desirable first to collect all the information available from a study of natural conditions.

A number of difficulties in the method adopted become at once apparent. One of these is that after measuring the factors on the sites where a certain species thrives and on other sites where it does not occur, we can not always be absolutely sure that its absence on the latter sites is not due to non-introduction, or to competition with other species rather than to adverse factors in the habitat itself. In the case of widely separated habitats these questions may become serious ones, but when the study is confined to one locality they can usually be disposed of. The question of introduction is at once eliminated. Opportunities are usually found for securing evidence as to whether or not competition is an important factor. In order further to eliminate the possibility of error, the study of natural distribution has been supplemented by planting a number of species in habitats where they do not occur naturally.

The greatest problem arises from the fact that the transition from one site to another involves changes in several physical factors. The question then to be decided is, which factor is the limiting one? Usually a general knowledge of the occurrence and requirements of the species will aid in arriving at a decision, but in some cases direct experimental data are required. The planting experiments just mentioned will throw considerable light on the subject. If the planting fails, the appearance of the plants will often furnish a clue to the cause of their death. If the plants grow on a site where the species does not occur naturally, it may indicate failure of seed to have reached the site in question by natural methods, or circumstances adverse to germination and early establishment of seedlings, or possibly inability to compete successfully; or it may indicate that climatic conditions for the period of the experiment have been unusually favorable and that therefore success is only temporary.

Change of site in this region usually means a change in altitude or slope exposure. In either case the physical factors mainly concerned are temperature and moisture. Soil appears to be important in this region only in so far as it affects available moisture supply. From this standpoint it is very important and undoubtedly deserves more attention than it has received in this study. Light is determined mainly by density of cover and is therefore under control for experimental purposes.[12]

There is a certain well defined relation between temperature and moisture conditions which, with a few local exceptions, holds for all the forest types. An increase in elevation or change to northerly aspect is accompanied by falling temperature and rising soil and atmospheric moisture, while the opposite changes in altitude or aspect are accompanied by rising temperature and decreasing moisture. The changes in both temperature and moisture manifest themselves in several ways. A change in seasonal temperature involves first a change in the quantity of heat energy available for carrying on plant activities, and secondly in the duration of the growing season as determined by the period in which effective growing temperatures occur and the absence of frosts and snow. Moisture supply is determined by precipitation, by storage in the soil in a form available for plant use, and by evaporation. The last named factor is in turn determined by temperature, wind and relative humidity. Temperature is most important not only in determining the rate of evaporation, but also, by controlling the rate of melting of snow, greatly affects the absorbtive capacity of the soil. The effect of temperature upon the melting of snow is of tremendous importance in regulating growing conditions in this region. The abundance of moisture which makes possible the luxuriant spruce forests, for instance, is due not so much to high precipitation as to the fact that the winter precipitation comes mainly in the form of snow which lies on the ground until well into the month of June. By the time the snow is gone, the soil is saturated and summer temperatures are at hand. The result is immediate growth and a maximum utilization of moisture. In the yellow pine type, on the other hand, the snow usually disappears by April, but active growing temperatures seldom come until after May 15. The result is that most of the moisture in the upper foot of soil is evaporated before plants can use it.[13] From the foregoing it becomes obvious that temperature and moisture as factors controlling plant growth are almost inseparable in nature, and that although the direct effect of moisture is more obvious, temperature is really the dominant factor because it virtually controls moisture.

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[12] [Is it not possible that with the differences in elevation involved in this study there may be sufficient differences in the intensity of solar radiation to play an important part? It may be, however, that the increase in solar radiation with altitude is largely masked by the increase in the moisture vapor of the air at the higher elevations. —EDITOR.]

The temperature data employed in this study are air temperatures. It is generally recognized that air temperature is but a rough expression of the heat energy absorbed and utilized by the plant. It is also evident that measurements of total solar radiation would not give the results desired by plant physiologists. The writer has approached the problem in a preliminary way by measuring transpiration in potted tree seedlings, but the work has not been carried sufficiently to warrant definite conclusions as to its practicability.

On the basis of existing knowledge regarding the natural occurrence of various tree species in this region, the tentative conclusion has been formed that the upper altitudinal range of all species is determined by low temperature and the lower range by deficiency in moisture. In other words a species belonging to a given forest type, on descending into the next lower type is arrested not by the higher temperature prevailing there, but by the deficiency in moisture; on the other hand, on ascending into altitudes above its natural habitat, it encounters unfavorable conditions not in the increased moisture supply but in the lowered heat supply. This hypothesis agrees with the findings of Shreve[14] in the Santa Catalina Mountains of southern Arizona, but is contrary to the conclusions of Bates[15] whose studies in the central Rocky Mountains point to low winter temperature of the soils as the upper control, and high air temperature as the lower control.

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[13] [Although the melting snows penetrate deeply into the less pervious soils of the open areas known as "parks," the summer rains apparently do not, and it is probable that the porosity of the different soils—both on account of moisture and soil aëration—is important in determining whether or not trees will succeed.—EDITOR.]

[14] Shreve, Forrest. "The Vegetation of a Desert Mountain Range as Conditioned by Climatic Factors," Carnegie Inst. of Washington, Publ. 317, 1917.

[15] Bates, C. G. "Forest Types of the Central Rocky Mountains" (to be published by the U. S. Weather Bureau).

In order to proceed intelligently with a discussion of this subject, it is necessary to define our conception of temperature and moisture in their relation to the problem at hand. By temperature is meant the heat supply as determined by solar radiation and air temperature, and imperfectly expressed by the temperature of the air and soil. By moisture is meant the balance between moisture supply and consumption which might be expressed by the ratio between available soil moisture and transpiration.

The aspects of temperature with which we are primarily concerned are its availability as a source of energy for photosynthesis and transpiration, its relation to absorption and other vital processes, and injurious effects due to excessively high temperature.

The ability of a plant to carry on photosynthesis and assimilation with a low heat supply is believed to be the dominant factor in deciding whether or not it can exist in the high altitudes of this region. That plants differ widely in their heat requirements is a matter of common observation. For example a number of herbaceous plants commonly blossom before the snow is entirely gone while others show no signs of activity whatever.

Transpiration need be considered here only when it occurs in excess. Under this condition temperature transforms itself into a moisture factor, and to that extent the effects of temperature and moisture are inseparable. The relation is further complicated by the fact that in this region an increase in temperature is always accompanied by a decrease in precipitation as well as by an increase in evaporation; and a decrease in temperature is accompanied by an increase in precipitation and a decrease in evaporation. Therefore when moisture deficiency is cited as the limiting factor in the downward extension of a species, it must be recognized that we are dealing not only with deficient moisture supply resulting from low percipitation, but also with excessive water consumption due mainly to high temperature.

Injuries from overheating are closely related to and often indistinguishable from drought injury. It may be assumed that transpiration, by its cooling effect, tends to prevent the occurrence of excessive temperature within the plant tissues, and therefore it is quite probable that within certain limits an increase of water supply sufficient to maintain the maximum transpiration rate will mitigate the injurious effects of high temperature. It is known that certain species, such as the western yellow pine, the junipers, and Arizona cypress are capable of withstanding much higher atmospheric temperatures than prevail in their native habitats, providing that they are well watered. Arizona cypress in particular has shown itself remarkably adaptable in this respect. This tree normally grows in the mountains where maximum temperatures rarely exceed 95 degrees F., but under irrigation it thrives in localities where maximum temperatures rise to 120 degrees F. On the other hand, species like Engelmann spruce and Douglas fir appear to have decided limitations in regard to endurance of high temperature.

We have seen from the preceding discussion that when the downward extension of a tree is attributed to deficient moisture we are also dealing with high temperature, and therefore strictly speaking moisture alone can not be regarded as the limiting factor. Moreover, beyond certain temperature limits heat regardless of moisture may be the limiting factor. What we are concerned with in this study, however, is the actual rather than the ultimate barrier. If, after eliminating other conditions, we find that a plant has all the moisture it can use and still fails, we may assume that it has encountered its limitation in heat conditions. If, on the other hand, the moisture supply is known to be near the minimum and the temperature well within the limits for the species, it may be concluded that moisture is the limiting factor. The following practical test has been applied in this study. When a species is transplanted below its natural range into a hotter and drier climate, if it succumbs under natural conditions but thrives when the moisture supply is increased by cultivation or watering, lack of moisture is regarded as the condition responsible for the failure of the species to descend below its present range.

In the following pages the range of each of the coniferous species of this locality will be discussed from the standpoint of limiting factors.

PINON-JUNIPER TYPE.—The pinon (*Pinus edulis*), two junipers (*J. utahensis* and *J. monosperma*), and a third juniper (*J. pachyphloca*) which is of limited occurrence, form a woodland belt representing the transition from desert to timber forest. Their characteristic low form and open stand adapt them to the arid conditions of this type. All the evidence at hand points to deficient moisture as the factor limiting their encroachment upon the desert, and low temperature as the factor checking their ascent into the yellow pine type where moisture conditions are more favorable for vegetation in general. The woodland is approached from the east in this region along the Santa Fe Railroad west of Winslow, on a very gradual ascent. The first suggestion of an approaching forest is indicated at about 5,000 feet elevation by straggling junipers scarcely more than a foot high. Four or five miles farther on the junipers become distinctly more prominent in both numbers and development but continue to be undersized. Normal development is attained at an elevation of a little over 6,000 feet. The pinon makes its appearance at a somewhat higher altitude than the junipers. At about 6,500 feet, both the junipers and the pinon have attained their maximum development. Here the western yellow pine (*P. ponderosa scopulorum*) becomes conspicuous as a low bushy tree. Ascending to 6,700 feet the yellow pine increases in size and numbers, while the pinon and the junipers become less abundant, though still maintaining good size. At this point the alligator juniper (*J. pachyphloea*) makes its appearance. It persists well up into the yellow pine type, thus indicating a higher moisture and lower temperature requirement than the other two members of the genus. The mean annual rainfall at the lower and upper limits of the pinon-juniper type are about 10 and 18 inches respectively. Of hardly less importance is the depth of the soil. At the lower limits in certain localities, bedrock is encountered within 2 or 3 inches of the surface while at the upper limit it is 2 or more feet below. In this case both precipitation and depth of soil increase the moisture supply in the higher altitudes. Farther east toward Winslow the soil becomes deep, but precipitation decreases, and here the trees are absent. On the western slopes of the Colorado Plateau the lower limits of the pinon-juniper are less distinct owing to a more varied topography.

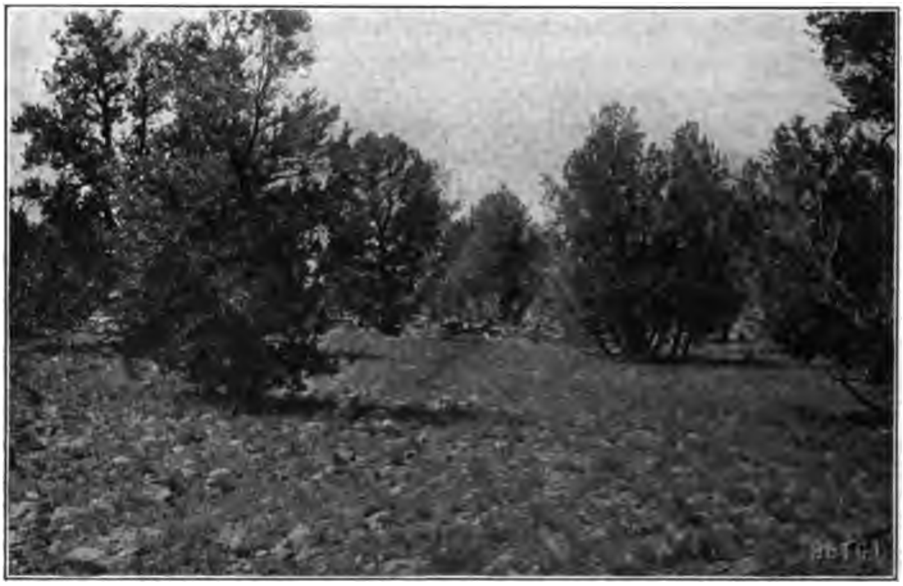

FIG. 9. Pinon-juniper type, showing open character and form of trees.

That lack of moisture rather than excessive heat or unfavorable soil composition prevents the growth of the woodland species in low altitudes is shown by the fact that sizeable specimens occur along water courses well below the general limits of the woodland. The fact that these trees respond to cultivation and irrigation by greatly increased growth is ample evidence that the higher soil moisture of the yellow pine type is not unfavorable to them. Nor is competition a limiting factor because there are any number of openings in the yellow pine forest where they would encounter neither root nor crown competition. Moreover the junipers commonly reproduce in the shade of older trees in their natural habitat. There is abundant evidence, however, that low temperature, through its effect on photosynthetic activity, is the limiting factor. Wherever a pinon or a juniper occurs above the middle altitudes of the yellow pine type, it is invariably on a southerly exposure. The same observation has been made by Robbins[16] in Colorado. Fairly large specimens have been observed in sunny, protected situations as high as 7,300 feet. Pinons grown from seed and later field planted in the vicinity of the Fort Valley Experiment Station still persist after five years, but are not thrifty.

YELLOW PINE TYPE.—Western Yellow Pine (*Pinus ponderosa scopulorum*) occurs in pure or almost pure stands throughout the type. In fact it dominates so completely that the few associated species are seldom mentioned as being a part of the stand. At the upper and lower extremes of its range it exhibits much the same characteristics as the woodland species. Isolated specimens occurring in the pinon-juniper type, though sometimes of large diameter and apparently several hundred years old, are usually of low stature unless found along a water course, in which case they reach fairly good height. Planted trees far below the natural range make a tremendous height growth under irrigation, but without irrigation or cultivation they almost invariably die during the first or second season. In its extreme upper range it is confined to southerly exposures. Specimens observed in such situations are

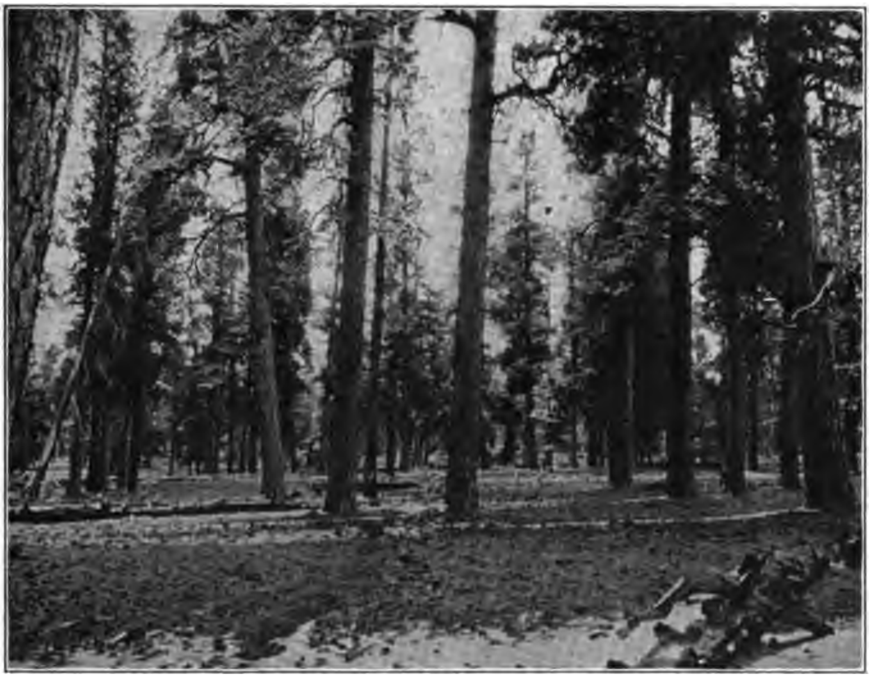

FIG. 10. Yellow pine type. Meteorological station in the background.

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[16] Robbins, Wilfred W. "Native Vegetation and Climate of Colorado in their Relation to Agriculture," Colo. Agr. College, Bul. 224, 1917.

sometimes of good size but produce few cones. This condition was conspicuous in 1918 which was an exceptionally good seed year in the yellow pine type. Plantings were made in 1918 in all the forest types above the pinon-juniper up to the Engelmann spruce type. In every case the survival to date is fairly good, and, excepting in the Engelmann spruce type, fairly good height growth has resulted. A noticeable feature, however, is that in the Engelmann spruce type the length of the needles formed during 1918 was below normal. On a north slope in the spruce type, yellow pine plants placed in a small opening where they received about 5 hours of direct sunlight per day during June, July, and August scarcely more than opened their buds, and developed only mere rudiments of needles. On a southerly exposure nearby, in a larger opening receiving practically full sunlight during June, July, and August height growth was almost equal to that in the yellow pine type, but the needles were decidedly below normal length. Seed sown in a well prepared bed in this opening showed only 6 percent germination, while seed from the same lot sown in the yellow pine type gave 67 percent. Seed of Engelmann spruce and bristle-cone pine sown in the above opening gave practically the same germination as in the greenhouse under a mean temperature of about 70 degrees F. It is interesting in this connection to note that hardy root crops, such as carrots and turnips, did not mature. The vegetative growth was decidedly below normal height, though of rich green color. Beans grow only 3 or 4 inches tall, had poorly developed leaves, and did not blossom, although they remained uninjured by frost until September 17 and were not killed until October 17. In the yellow pine type 3,200 feet lower beans made a luxuriant growth and fruited freely up to August 17, when they were severely injured by frost and were finally killed by frost on September 17. From the foregoing examples it becomes evident that, although the frostless season was some 30 days[17] longer in the Engelmann spruce type, the temperature was too low for yellow pine. As has been previously pointed out, the extreme minimum temperatures are usually lower in the yellow pine type than in the Engelmann spruce type. The vital temperature deficiency in the Engelmann spruce type with reference to growth of yellow pine lies in the low maxima. In other words, effective temperatures for plants of medium to high heat requirements are seldom reached or are of too short duration for good growth. This is illustrated by the record of maximum temperature and the total number of hours with temperature above 70 degrees F., as shown in the following table and in figure 3, Part I.

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[17] Table 6 in part I shows a difference of only 8 days in the 1918 frostless period. This table, however, is based upon temperatures of 32° or below. Tender plants are often frosted when the temperature recorded in a standard Weather Bureau shelter is one or two degrees above 32° F.

Forest type	Mean maximum temperature (1918), Degrees F.					Total No. hours 70° and Above (1918)
	May	June	July	Aug.	Sept.	
Yellow pine type (Fort Valley)	60.2	79.8	75.1	73.8	72.3	633
Eng. spruce type, NW slope, cover	45.6	62.3	59.0	57.9	54.0	4
Sw slope, open[18]	48.0	65.0	60.7	59.7	59.2	70[18]

Soil temperature is a further index of the heat supply. Comparable records are available at all the stations only for the period July–September, but these are sufficient to indicate a great difference in the heat available during the growing season. Heat supply during the growing season is directly related to the ability of the plant to carry on photosynthesis. What may be of equal importance is the period during the winter months when the soil remains frozen, or at a temperature so low that the moisture can not be absorbed by roots. On northerly exposures in the Engelmann spruce type the soil temperature is continually below 32 degrees F. from about December 1 to June 1, while in the yellow pine type the period is much shorter, usually not over 60 to 90 days. The presence of salts in the soil water tends to lower the freezing point; how low the temperature can fall without freezing the soil water depends upon the strength of the solution. Observations by Sampson at the Great Basin Experiment Station in Utah and by the writer at the Fort Valley Experiment Station indicate that the soil does not ordinarily freeze until a temperature of 30 to 31 degrees F. is reached. According to investigations by Kihlman,[19] the soil moisture ceases to become available to plants at a temperature of 1° C. (1.8° F.) above the normal freezing point.

A casual experiment during the winter of 1918–19 throws considerable light on this question. Four 4-year-old yellow pines and one 5-year-old bristle-cone pine used for transpiration experiments in the Engelmann spruce type were stored in a log cabin over winter. All the plants were in 4-inch sealed iron pots. The available moisture supply was kept at about 8 percent by occasional fillings. Early in May, 1919, an examination revealed that all of the yellow pines were dead, while the bristle-cone pine was in perfect condition. A weighing of the pots at this time showed the soil to be up to the standard moisture content. The only apparent explanation for the results is that the pots were frozen solid from December 1 to May 1 and thus no moisture was available to the roots. During this period transpiration, slight as it was, was sufficient to kill the yellow pines. The bristle-cone pine, however, because of greater resistance to transpiration, or because of greater endurance of desiccation, was uninjured. Yellow pine, bristle-cone pine, limber pine, Douglas fir and Engelmann spruce planted in the soil under natural conditions outside the cabin where they were covered through the entire winter by several feet of snow lived through in good condition excepting that 3 out of the 5 yellow pines and a smaller percentage of Douglas fir and Engelmann spruce had dead terminals. It is quite probable that the injury to the terminals occurred before the first heavy snowfall when the soil was frozen but the snow was not deep enough to cover the plants completely. These observations indicate that yellow pine is more subject to winter killing than is limber pine or bristle-cone pine.

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[18] Interpolated in part.

[19] Kihlman, A. Osw. "Pflanzenbiologische Studien aus Russich Lapland." Acta. Soc. pro Fauna et Flora fennica. 6: 1–263, 1890.

Sachs found that cooling the soil to a point slightly above freezing slowed down the water absorption of *Phaseolus, Nicotiana,* and *Cucurbita* until wilting occurred. Kihlman confirmed Sach's results, using *Cucurbita pepo,* 3 pots of which were packed in ice, with a control pot in sawdust. When the soil in the ice-packed pots dropped to 1° C. the three turgescent plants were exposed to the sun and wind at a 12° C. air temperature. Two hours later the plants in the ice-packed pots were all wilted. The soil in one of these was then warmed to 25–28° within 15 minutes by adding lukewarm water, and kept at this temperature. In spite of increasing air temperature and wind velocity, the plants had almost recovered their turgidity within four hours. Adding 10–12° water to another pot produced a slow change, but turgidity was restored by the following morning. A third pot was left longer on ice, the plant in consequence showing greater injury, the cotyledons never wholly recovering turgidity. No mention is made of the control pot; apparently these plants did not wilt. (From abstract by E. C. Rogers.)

The following table gives a comparison of soil temperatures within and above the natural range of yellow pine.

	Altitude	Aspect	Cover	Soil Temp. 12″ July–Sept., 1918, degrees F.	No. of days with soil temp. 32° F. or lower winter 1917–18, depth	
					12″	24″
Yellow pine type........	7,300	Level	Open	65	48	10
		"	Partial cover	59		
		"	Dense cover	57		
Douglas fir type........						
Last yellow pine....	8,900	South	Open	57	58	20
No yellow pine.....	8.900	NW	Partial cover	51		
" " "	10,000	South	Open	55		
Engelmann spruce......						
Open..............	10,500	SW	Open	52		
Cover..............	10,500	NW	Dense	45	182	156

Transpiration furnishes a more direct comparison of the relative amounts of heat utilized. Two series of 3-year-old plants (A containing 6, and B 3 plants) were run during a period of six weeks, from August 21 to September 30. Both series were exposed to open air conditions at the Fort Valley Experiment Station from August 21 to September 19. On September 20 Series B was taken to the Engelmann spruce type and placed in an opening where the plants were exposed to practically full sunlight. The results follow:

	Mean daily transpiration per plant, gr.		
	Aug. 21–Sept. 19	Sept. 21–30	Decrease second period
Series A (in Y. P. type continually)	3.83	3.63	5%
Series B (in spruce type Sept. 21–30)	4.36	3.00	31%

The above figures indicate a reduction of the transpiration rate by 26 percent as a result of moving the plants to the Engelmann spruce type. Although the study has not been carried far enough to determine the relative effects of different factors our knowledge of the conditions suggests temperature as playing the leading rôle.

Data now at hand show quite conclusively that yellow pine will not thrive in temperatures as low as those encountered in the Engelmann spruce type, unless it be in the extreme lower portions. The indications are that the possible extreme upper range of the species conforms closely to its present occurrence. This is being checked by two planting and instrument stations between the uppermost yellow pine and the Engelmann spruce type.

Douglas Fir Type.—Unlike yellow pine, Douglas Fir (*Pseudotsuga taxifolia*) occupies the sites most free from rigorous climatic conditions. The temperature, though low (mean annual for 1917 and 1917 41.7° F.) is characterized by great moderation. Frosts are of rare occurrence during the growing season. The frostless period is almost as long as in the pinon-juniper type 3,000 feet lower. Precipitation is practically equal to that of the Engelmann spruce type, and soil moisture is sufficient for all but the plants of distinctly high moisture requirements. Our knowledge of the characteristics of Douglas fir indicates that its occupation of these favorable sites is dictated by the requirements of the species.

Frost damage is one of the commonest difficulties encountered when Douglas fir is taken outside its natural habitat. In nursery culture sensitiveness to frost is always a factor to reckon with in the Rocky Mountain region. Much the same difficulty is experienced in the eastern states. The species has been extensively introduced in Europe where frost injury is recognized as one of the main difficulties in its propagation. Douglas fir seedlings respond very quickly to the first warm days of spring. The tender shoots are later killed by frosts which are apt to occur late in May or early June. It is therefore not mere coincidence that this species occupies the climatic zone which in this region is least subject to unseasonable frost.

Douglas fir is also subject to winter killing. According to available information the damage takes place during temporary periods of sunny weather in the winter time when the soil is frozen. At such times the transpiration becomes active but soil moisture is not available to the roots. Douglas fir plants grown in nurseries in the yellow pine type almost invariably winter kill unless the tops are covered. Yellow pine in the same nurseries is rarely injured. In their native habitat Douglas fir seedlings are covered by snow throughout the winter and early spring. They are also shaded by the aspen in whose shelter they commonly grow.

Another peculiarity of Douglas fir is that the tops frequently dry up when exposed to strong sunlight, even when the soil has a fairly high available water content. For this reason seedlings and transplants grown in nurseries must be shaded. Douglas fir plantations suffer severely in open spots, while adjoining aspen-covered plots are uninjured. Whether the injury is due to superheating of the tissues or to disturbance of the proper balance between water loss and water absorption is more or less of an open question. Obviously the maintenance of a vigorous transpiration stream would tend to prevent superheating; on the other hand, it is conceivable that a plant may be so constituted that even though the water supply at the roots is at an optimum, it can not maintain transpiration at a rate sufficiently high to prevent excessive leaf temperatures. Douglas fir apparently has distinct limitations in this respect, but whether its absence in the yellow pine type or even in the pinon-juniper type is accounted for by high temperature rather than low moisture supply is doubtful. The question can be answered by the simple experiment of planting a few Douglas firs in the lower types under conditions where they will have all the water they can utilize. In this connection, mention may be made of the fact that in transpiration experiments carried on last summer in the yellow pine type, Douglas fir and Engelmann spruce seedlings grown in pots where the available moisture content of the soil was not allowed to fall below about 8 percent, no evidence of injury was discernible. In the greenhouse, however, the leaves on some of the Douglas fir plants were injured when the temperature was allowed to rise to 100° F., while the Engelmann spruce alongside was uninjured.

Since frost, winter killing, and exposure to direct sunlight are most injurious in altitudes below the Douglas fir type, the question arises whether they, rather than merely a lack of soil moisture, may not account for limiting the downward extension of the species. It is known that the injuries described largely disappear after the seedling stage is passed. It is also known that artificially established Douglas fir seedlings thrive in the shelter of groups of yellow pine when given winter protection and water. It is reasonable to assume, therefore, that if soil moisture in the yellow pine type were adequate to support Douglas fir, the latter would struggle through the seedling stage by taking advantage of the protection afforded by groups of living trees and particularly of fallen trees. Its tolerance of shade would make this possible. As a matter of fact, this does happen in the upper portion of the type where moisture more nearly meets the requirements of Douglas fir. But this expedient is not sufficient to enable it to migrate far into the lower altitudes because deficient soil moisture together with high transpiration becomes a more and more unsurmountable obstacle.

Frost, winter killing, and injury from exposure to direct sunlight are far less active in checking the upward than the downward extension of Douglas fir. In the Engelmann spruce type, for example, frosts are but little more prevalent than in the Douglas fir type, and the range of temperature is far less. An equal or greater amount of protection is afforded by snow, underbrush, aspen and down timber. The remaining factor to be accounted for is heat.

The mean annual temperatures in the Douglas fir and Engelmann spruce types for the years 1917–1918 were 41.7° and 36.0° respectively (Table 1 in Part I). During the growing season, June to September, inclusive, the mean maxima were 67.1° and 58.2° respectively, and the total number of hours with temperature 70° or above, 169 and 2½ respectively (Table 8 in Part I). Douglas fir has been planted at the base stations in both forest types and at two intermediate stations. The plants are thrifty excepting at the Engelmann spruce base station on a northwest slope, where they have made but little growth. Present indications are that the heat supply in the Engelmann spruce type is deficient for Douglas fir.

Limber Pine.—Limber pine (*Pinus flexilis*) is associated with Douglas fir almost throughout the range of the latter; but limber pine is able to occupy wind-swept slopes and ridges where Douglas fir will not grow. Its ability to withstand strong insolation accompanied by high wind on steep southerly slopes at high altitudes is noteworthy. Special studies have been made on one such slope which ranges in elevation from about 9,300 to about 10,000 feet. During the growing season of 1918, the soil moisture on this slope ran slightly below that in the yellow pine type. The same was true of maximum air temperatures and mean soil temperatures. Wind movement was practically three times as high as in the yellow pine type. On the lower ⅝ of this slope limber pine is the only tree, and here it occurs only as scattered individuals. Near the top of the slope it begins to give way to bristle-cone pine (*Pinus aristata*) while across the ridge on a northerly aspect it is largely supplanted by Engelmann spruce. The evidence indicates that the upper limit of limber pine on this slope is determined by low temperature during the growing season. This point is, however, being checked by plantations in the Engelmann spruce type. The extreme lower range of the species in this locality extends well into the yellow pine type where its occurrence is limited to north slopes and canyon bottoms. Attempts to transplant the tree to the yellow pine type below its natural occurrence have failed excepting in 1918 when moisture conditions during the growing season were above normal. In the greenhouse where well watered, it has withstood a temperature of 100° F. without injury. These experiences indicate that the lower range is determined by deficient soil moisture rather than by high temperature.

ENGELMANN SPRUCE TYPE.—*Engelmann Spruce.*—Engelmann spruce (*Picea engelmanni*) exhibits a sensitiveness to frost, winter killing and strong sunlight similar to though less pronounced than that of Douglas fir. Throughout its range it avoids dry, sunny sites, particularly those exposed to high wind. The Engelmann spruce type, though having a shorter frostless period than the Douglas fir type, is generally free from frost during the growth season. The temperature rarely rises to the 70 degree mark, and is exceedingly constant; on typical spruce sites the daily range is seldom over 20° F. The deep snow cover between about December 1 and the middle of June renders frost and winter killing relatively harmless to reproduction. When the snow disappears, the danger of killing frost is practically past. Autumn frosts approach so gradually as seldom to cause damage to woody plants.

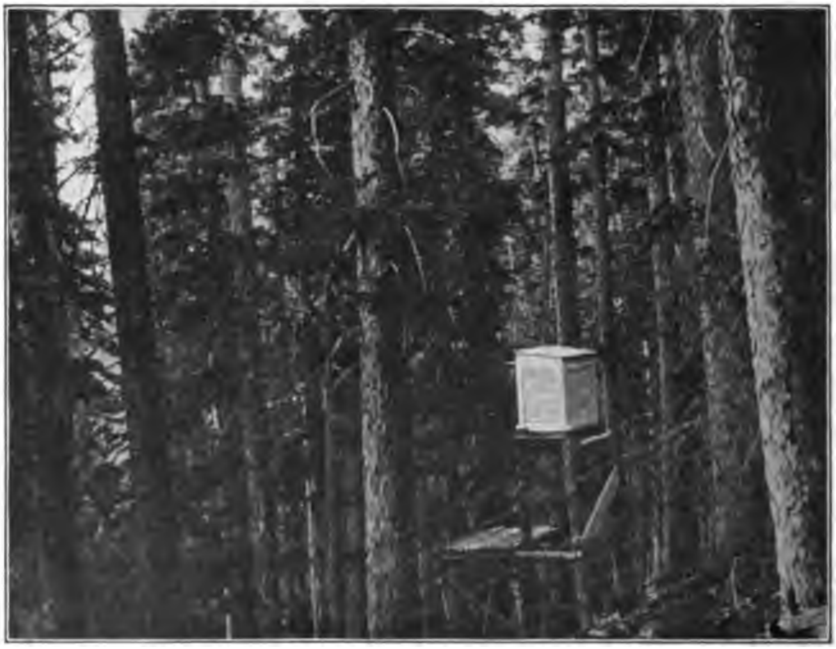

FIG. 11. Meteorological station in a mature forest of Engelmann spruce and cork-bark fir on a steep north slipe at 10,500 feet.

Engelmann spruce, like Douglas fir, appears to avoid high temperatures. Undoubtedly the injurious effects of excessive heat can, to a certain extent, be overcome by increasing the water supply; but observations indicate that this species as well as the Douglas fir has pronounced limitations in this respect.

Attempts to establish Engelmann spruce in the yellow pine type by planting have been, on the whole, unsuccessful. Some plants have survived two seasons, but their present appearance predicts failure. Shading and irrigation are beneficial especially when the two are combined.

The behavior of the spruce in the Douglas fir type is illustrated by the following experience. In 1912 a seedbed of Engelmann spruce was established in the shade of Douglas fir trees at 8,700 feet. An excellent stand of seedlings resulted. They received no water other than natural precipitation, but were covered during the winter. After two years it was evident that the plants were not growing as rapidly as they should, and therefore the bed was heavily thinned, with slightly beneficial results. At the age of three years a number of seedlings were transplanted into a more open situation in the shade of aspen. Winter protection continued, but the seedlings were not watered. At the end of five years it was evident that the plants were distinctly below normal size and in the sixth year they died. Throughout the entire course of the experiment there was no evidence of violent injury such as results from frost winter killing or too intense solar radiation. The conclusion therefore is that the plants suffered from deficient soil moisture combined with excessive transpiration.[20] In view of the fact that the precipitation in the Douglas fir type is practically the same as in the Engelmann spruce type, and there is no important difference in soil, differences in moisture conditions must be attributed to factors affecting transpiration and direct evaporation from the soil. Of these factors, temperature is undoubtedly the most important in this case. It should be noted, however, that the unfavorable action of high temperature is not direct, but indirect, through its influence upon moisture. As stated in the discussion of Douglas fir, Engelmann spruce has been observed to withstand temperatures of 100° F. when supplied with abundant moisture.

Engelmann spruce reaches its upper limit at timber line which in this study has been taken as marking the lower boundary of the alpine type. Timber line is here regarded as the line at which the trees cease to have the erect tree-like form. Both Engelmann spruce and bristle-cone pine persist in the bushy or trailing form several hundred feet above this point. Mean air temperature at the timber line station is only from 4 to 5 degrees lower than on the optimum spruce sites, while the mean maximum is but 3 degrees lower. The spruce bears fertile cones right up to the point where it becomes trailing. One specimen was found bearing cones about 300 feet above this point but since this observation was made after the time of seed dispersal, it is not known whether the seeds were fertile. Both spruce and bristle-cone pine, however, reproduce well at timber line. Saplings grow erect and with apparent vigor until they attain a height of 6 or 7 feet, above which the tops are killed back. This gives rise to the theory that the injury takes place in the winter time when everything below 6 or 7 feet is covered with snow. The dead terminals are frequently barked, which points to strong abrasive action resulting from the snow and sleet being driven against the stems by high winds. Sleet storms accompanied by violent wind are common at this altitude from October to May. During the winter months the loose snow sweeps along the frozen surface in a manner suggesting sand storms. Observations in the spring of 1919 furnished an excellent illustration of the effect of wind action during the preceding winter. The trees and saplings at timber line on a broad ridge bordering the south side of a deep canyon almost invariably had their needles killed on the north side toward the canyon while on the south and sunny side they were uninjured (in lower altitudes injury of this kind is usually worse on the sunny side of the tree). Although the prevailing winds in this section are from the southwest, at this point the movement during the preceding winter was prevailingly north or northwest, coming up the canyon as demonstrated by a much shallower deposit of snow on the edge of the ridge bordering the canyon than a hundred feet back toward the south. The obvious explanation of the browning of the foliage is that the winds dry out the tissues excessively during the long winter period when soil moisture is not available to the roots on account of low temperature.

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[20] [Is it not possible also that the lack of cold temperatures to which the tree is accustomed in its natural habitat has interfered with its metabolism? Rigg, in a paper to appear in the next issue, quotes Lidforss as suggesting that the large sugar content of evergreen leaves in winter is probably due to the activation of a diastolic enzyme by low temperature. It would seem therefore that low temperature, aside from its influence on transpiration, plays an important part in the metabolic processes of the plant and could well account for the gradual decline of the Engelmann spruce seedlings transplanted to the Douglas fir type.—EDITOR.]

It seems fairly well established that the upper limit of Engelmann spruce *in tree form* is generally determined not by deficient heat supply for elaboration of plant food,[21] but by conditions affecting moisture supply as controlled by low soil temperature, high evaporation, abrasive action of wind and snow, and in some cases lack of soil. The above statement does not apply to the species in the trailing form as it occurs several hundred feet above the point where it ceases to exist as a tree. As we ascend to about 12,000 feet on the south and west sides of the peak, both the spruce and the bristle-cone pine become reduced to small bushes, and finally disappear entirely. In many instances this condition may be attributed to lack of soil, but occasionally we find between the boulders pockets of fairly deep soil protected from wind and apparently favorable to tree growth in all respects excepting temperature. Thus it appears that the *final* upper limit of both Engelmann spruce and bristle-cone pine is determined by temperature.

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[21] [Summations of effective temperatures in the spruce type as compared with those in the alpine zone would help in further establishing or controverting this. Sampson (U. S. Dept. Agr. Bul. 700, 1918) indicates that effective temperature are of much importance.—EDITOR.]

Cork-Bark Fir.—Arizona cork-bark fir (*Abies arizonica*) is associated with Engelmann spruce throughout the latter's range until an altitude of about 11,000 feet is reached. Here the fir drops out on north slopes but continues a short distance on the more sunny exposures where protected from high winds. Its lower range is determined by the same conditions as those limiting the downward extension of Engelmann spruce. Its absence from the upper portion of the Engelmann spruce type is undoubtedly due to lack of heat for photosynthesis.

Bristle-cone Pine.—Bristle-cone pine (*Pinus aristata*) begins slightly higher than the Engelmann spruce, and persists to the same altitude as the latter. It rarely occurs on northerly exposures, due perhaps to the fact that on such sites it is shaded out by the spruce and fir, but it predominates on southerly exposures. Like the limber pine, it is able to maintain itself on wind-swept ridges and steep south slopes where its associates of other sites fail. Its lower altitudinal limit corresponds closely with the upper limit of limber pine, thus indicating a lower temperature and higher moisture requirement than the latter. Although it prevails on steep south slopes which suggest dry soil, it has been observed that the snow persists later on these sites than on limber pine sites and therefore it is quite likely that they enjoy more soil moisture than the latter.

In planting experiments in the yellow pine type during 1918, bristle-cone pine showed every indication of being perfectly adapted to its new habitat. This behavior may be due to the unusually heavy summer rainfall. It showed no evidence of injury from high temperature during the hottest periods of 1918 and 1919 when air temperatures mounted to as high as 89 degrees F. In the greenhouse it has under favorable moisture conditions been subjected to temperatures of 100° F. without evident injury.

The upper range on southerly exposures is apparently controlled by the same conditions as in the case of Engelmann spruce. On northerly aspects there is every indication of a limitation due to deficient heat supply. It is true that on such sites it is usually suppressed by the spruce, but the fact that it does not occur on northerly exposures above 11,000 feet even in openings indicates that it does not find favorable temperature conditions here.

Conclusions

The weight of evidence thus far accumulated in this study supports the hypothesis that the upper altitudinal range of all tree species in this region is determined by low temperature, and the lower altitudinal range by deficient moisture.

That low temperature, primarily as related to photo-synthesis, constitutes the upper control, seems established beyond serious doubt. This does not ignore the part played by winter killing resulting from excessive water loss at times when low soil temperature renders the moisture unavailable to the roots. Drought of this character may prove fatal to trees beyond the seedling stage, but in this region it will rarely affect seedlings in altitudes above the pinon-juniper type, for the reason that the ground usually remains deeply covered with snow during the period of dangerously low soil temperatures. If a species such as yellow pine should by any chance reach a height of 2 or 3 feet in the Engelmann spruce type, for instance (an attainment which winter conditions would permit) the probabilities are that it would eventually succumb to winter killing due to repeated dying back of the portion extending above the snow level. As a matter of fact, however, yellow pine or any other low altitude species does not occur in the Engelmann spruce type, even in the early seedling stage, for the reason that the temperature is too low for photosynthesis, to say nothing of germination.

When we attempt to decide which is the limiting factcor in the lower range the problem may become more complex. As explained above the effects of high temperature and low moisture are to a large extent inseparable. It is recognized that every species has its limit of high temperature endurance, but the evidence here deduced indicates that in actual practice the limit of drought endurance (considering resistance to water loss, ability to survive in a desiccated condition, and capacity for obtaining water) is reached before the temperature endurance is seriously taxed. For example, Engelmann spruce in this region reaches its extreme lower altitudinal limit at about 9,000 feet. If it is found by actual test that increased water supply will enable the spruce to grow in temperatures as high as those experienced in the yellow pine type at 7,500 feet, it is reasonable to conclude that the condition which prevents the spruce from descending below its present range is deficient moisture rather than excessive heat. This sort of test is being made with all but two or three of the native species. The results thus far have shown that all are able to withstand temperatures far in excess of those experienced at the lower limits of their present range. These tests are being continued with a view toward securing conclusive data.

SUMMARY

1. Air temperature in the San Francisco Mountain region decreases rather uniformly with a rise in altitude excepting for local inversions in the minimum which occur between the yellow pine and the Douglas fir types, due to air drainage. The lowest absolute minima and the shortest frostless season occur in the yellow pine type, followed closely by the alpine type. The highest temperatures and greatest duration of high temperatures are found in the lowest altitudes. Maximum temperatures decrease uniformly from the lowest to the highest stations. The daily range is greatest in the lower altitudes, decreasing from about 50° F. in the pinon-juniper to about 20° F. in the Engelmann spruce. From the Engelmann spruce type to timber line there is a noticeable increase in range due to the exposed situation of the timber line station.

2. Precipitation increases rapidly with altitude up to the Douglas fir type. From the Douglas fir to the Engelmann spruce type it remains almost stationary, but at timber line there appears to be a substantial increase. On account of the great variability of precipitation a record of 2 years is not sufficient to establish a definite relation between the various forest types. All the types have about the same annual distribution which is roughly as follows: winter (Dec.-Mar.) 40 percent; spring (Apr.-May) 10 percent; summer (June-Aug.) 30 percent; autumn (Sept.-Nov.) 20 percent.

3. Wind movement is normally greatest in the higher altitudes, but this relation is not always indicated for the reason that some of the stations are located in the forest while others are in the open. The highest records are obtained at timber line which is entirely exposed, and the lowest in the spruce forest.

4. Evaporation records in this study show no constant relation to altitude, because wind movement and exposure to sunshine, two of the strongest factors influencing evaporation, vary at the different stations according to density of cover. The highest records obtained are in the pinon-juniper type, and the lowest in the Engelmann spruce type.

5. On the basis of origin there are several general soil types in this region. Those in the pinon-juniper type are derived from sandstone, limestone and basalt. In the yellow pine type local areas of limestone and sandstone occur near the lower limits but basaltic soils predominate over the type as a whole. Above the yellow pine type all the soils are derived from volcanic rocks.

Probably the most important soil character to be dealt with in this region is the capacity for absorbing and delivering moisture as determined by permeability, water holding capacity, and wilting coefficient. From this standpoint, the heavy clay soils common through the yellow pine type present the least favorable conditions for growth, particularly with respect to natural reproduction. Although these soils have a high water holding capacity, they also have a high wilting coefficient, and unless mixed with a large proportion of stone and gravel they are exceedingly impervious. High precipitation, low evaporation, and a high degree of permeability tend to create a large moisture supply in the Douglas fir and Engelmann spruce and Alpine types. At times of maximum vegetative activity, however, the available moisture supply in the Douglas fir and Engelmann spruce types may, on account of the heavy demands of the dense stands of trees, be reduced almost as low as in the forest types of relatively low precipitation and high evaporation.

Soil temperatures is of importance mainly through its indirect effects. When the soil temperature falls to 32° F. or even a few degrees above 32°, the soil moisture ceases to be available to plant roots. If this conditions persists continuously over long periods during which transpiration is favored by sunshine and wind the result may be fatal to a tree which is unable to endure extreme desiccation.

6. The data obtained in this study indicate that the upper limits of all the forest types are determined primarily by low temperature as related to photosynthesis, and that the lower limits are determined primarily by deficient moisture supply. Low soil temperature, by rendering the soil moisture unavailable to the roots, may under certain conditions as at timber line become the upper control; but, at least as far as reproduction is concerned, this is not believed to be a prevalent factor in this region, for the reason that in the high altitudes, the only places where long periods of continuously low soil temperature occur, transpiration in seedlings is reduced to a negligible quantity by a deep snow cover. Deficient moisture rather than high temperature is regarded as the lower control because observations supported by experimental data on nearly all of the species in this region indicate that when adequately supplied with moisture they are capable of enduring high temperatures far in excess of those which occur at the lower limits of their natural range.

NOTE: The foregoing article was originally prepared a year and a-half ago. Meteorological records were continued up to December 31, 1920, and investigations on other phases of the subject are still in progress as the article goes to press. While subsequent data have not appreciably modified the conclusions here presented they will permit more exhaustive treatment in a forthcoming publication.—AUTHOR.

NOTES AND COMMENT

Behavior of Loon and Sardines

While working on the outer end of our pier, about 1000 feet from shore, at 7.50 a.m. December 29, 1919, my attention was attracted to a small school of small sardines (*Sardinella coeruleus* Starks and Morris) quite conspicuous in the moderately clear water. The little fish seemed to be badly frightened. The school was very compact and was in the form of a symmetrical ball approximately six feet in diameter. The general course of movement was very regular but mainly toward the northwest and at an average depth of about ten feet. From 7.50 to 7.55 it was within a distance of twenty-five feet from the pier in a remarkably good position for observation.

Shortly after the school was noticed, a large loon (*Gavia immer* Brünnich) was seen about five yards distant resting at the surface. The loon dived and dashed toward the fish, swimming with feet only, the wings being held tightly against the body. The sphere of fish indented like a hollow rubber ball at the point of attack, then scattered slightly, coming together again into a sphere as the bird passed to the other side. The loon made several rushes at the sphere before coming to the surface for air. At one time it came up toward the middle of the school from below. The school spread into an almost perfect circle through the center of which the bird swam.

Most tries were made by dashes at the sides of the sphere. After coming to the surface the loon almost instantly thrust its head under, then dived soon after. Six or eight under water trips were made by the loon while still close enough to be plainly seen. Apparently no fish were caught at any time. Swimming was entirely by the feet in every case. Sometimes the bird made one look below the surface before diving, at other times two or three looks. The school of fish stayed in about the same spot for five minutes.

At the time that the performers in this drama of life drifted from sight there was no evidence that the loon had made a single catch. One might suggest the possibility that the bird was unable to make a choice amongst so many chances before his opportunity was gone. Members of the Station staff have noticed on other occasions the symmetry of form of small schools of sardines, the perfect coordination of movement in evolutions of the school whether in avoiding objects or in leisurely change of direction, and the tendency to instant re-formation when unavoidably scattered by several enemies. Dr. W. E. Ritter raises the question as to whether these group movements of sardines may not be protective adaptations in behavior, useful through confusing enemies by distribution of individuals equidistantly from the point of danger in a symmetrical figure.—W. E. ALLEN, *Scripps Institution for Biological Research of the University of California, La Jolla, California.*

BEHAVIOR OF FEEDING MACKEREL

On September 6, 1920, at 8.15 a.m., I was engaged in taking a daily plankton collection at the outer end of the pier. While so occupied I noticed a mackerel (*Scomber japonicus* Houttuyn) of about one pound weight, dashing through the water with a freshly caught sardine (*Sardinella coeruleus* Starks and Morris) of about three inches length, held crosswise in its mouth. In a moment other mackerel were seen rushing from all sides toward the one which had made the capture. They snatched at the projecting ends of the sardine and in an instant the water was aboil with mackerel fighting over the broken bits of dismembred prey. The general scuffle and scramble was somewhat similar to that of chickens about a captured worm, or gulls about a stolen fish, but there was much more of an appearance of reckless ferocity.

Flurries such as that caused by this group had been frequently seen near the pier during the first week in September, but in no other case had it been possible to see the beginning of the contest. Since there were many sardines in the water all about this group of mackered, and since enormous numbers had been seen in the areas of similar flurries, it seems fairly clear that mackerel as well as many other anmals will not work for or hunt for their own food if there is any possibility of robbing a neighbor.

In this connection it is worth while to remember that the exquisitely coordinated movements of a school of sardines seem baffling to mackered and sharks in the same way as it seemed to be in the case of a loon described in the foregoing note. Apparently a conspicuous sardine would be instantly selected for slaughter. All hope of survival seems to lie in rigid conformity to type. Does any one know whether such fishes as sardines are less variable than are the predatory fishes?—W. E. ALLEN, *Scripps Institution for Biological Research of the University of California, La Jolla, California.*

THE NATIONAL PARKS

The Ecological Society fully realizes the need of preserving natural areas for scientific and educational purposes; this means not only setting aside new areas but keeping intact those already reserved. We already have in the United States nineteen National Parks and a larger number of National Monuments in which, for the most part, natural conditions prevail. These wild regions, some of them set aside many years ago, are as yet practically untouched and are, in fact, nature museums. Scientific men, more than any others, are interested in the effort to protect these parks from being turned over to commercial development; for while the invasion of the parks will interfere with the recreation and, to a less extent, with the physical well-being of a portion of the public, it may very well interrupt and make impossible forever scientific inquiry of great importance.

Recently there have been not a few attempts to secure these parks or portions of them for commercial uses; and these efforts not only endanger the scientific and educational purposes of the parks, but have a far-reaching influence in their possible encroachments on the scenic and recreational aspects in which the general public is so deeply concerned.

The passage of the Federal Water Power Bill, which empowers a Commission to grant licenses for the construction, in National Parks and National Monuments, of reservoirs, irrigating ditches, power lines, and plants in connection with such development, is the most immediate danger to these natural areas. National Parks and National Monuments should be excepted from the provisions of this law.

The National Parks Committee, on which are represented the organizations desiring the preservation of the Parks, including the Ecological Society, is asking all interested organizations to cooperate in preventing these encroachments.

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